THE RELATIONSHIPS OF THE SALAMANDERS OF THE GENUS *PLETHODON*

By

RICHARD HIGHTON

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INTRODUCTION

The North American genus Plethodon presently has more recognized forms than any other genus of salamanders. It is the type genus of the lungless family Plethodontidae, reviewed so ably by Dunn in 1926. At present, this is the most successful salamander family; over half of the living species of the Order Caudata are plethodontids. North America is the center of the distribution of the family, but one genus, Hydromantes, also occurs in Europe, and members of several genera enter the Neotropical region. Salamanders of this family occupy habitats, ranging from strictly aquatic cavernicoles (Typhlomolge and Haideotriton) and mountain stream dwellers (Leurognathus) to others like Plethodon, which are completely terrestrial, even to the extent of laying their eggs on land. Dunn believed that Plethodon is the most primitive genus in the attached-tongue branch of the family, and that Hemidactylium, Ensatina, Batrachoseps, and Aneides are more specialized derivatives of a Plethodon-like ancestor.

In 1926, only eleven forms of Plethodon were known to Dunn. In 1943, Bishop listed 17 species (one has since been removed from the genus) and two subspecies (both are now considered different species). In 1944, Grobman reviewed the distribution and relationships of the eastern section of the genus, including some sixteen species and subspecies. There are now twenty-five forms recognized in eastern North America, with seven more in the western United States and Canada.

Grobman (1944: 266) divided the eastern forms into two groups, the Large Plethodons and the Small Plethodons. He suggested that these

groups might actually represent distinct genera or subgenera, but he reserved judgement in this matter until the relationship of the western species with the eastern forms could be determined. One of the purposes of the present study is to determine these relationships by a comparative study of the morphology of all the species of the genus Plethodon.

Of the twenty-five genera in the family Plethodontidae, only two others show as great or greater disjunctions in their distributions as that found in Plethodon. These are Hydromantes, with two forms in Europe and three species in California, and Aneides, with four species in western North America and one in the Appalachian Mountains of the eastern United States. In the past two decades, several new plethodons have been discovered in both eastern and western North America. A review of the relationships of these forms offers a valuable opportunity to study the evolution of this important group of North American salamanders.

The importance of examining plethodons in life has been emphasized by most recent workers. Many species, particularly the Large Eastern forms, are extremely difficult to identify after years of preservation. In few other vertebrates are differential characters between species so rare. For this reason, a special attempt was made to obtain living specimens of each form. Twenty-five of the thirty-two forms recognized herein have been studied alive.

The list of persons who have contributed specimens to this project is long and I wish to express to each of them my sincerest thanks and appreciation for their valuable aid: Charles G. Adams,

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Most of the material given me by these persons has been deposited in the University of Florida collection. This collection has formed the nucleus of the material on which this study is based. Some additional specimens have been borrowed from other collections, but I did not attempt to follow the course of the conventional monographer and examine every specimen available in museums, simply for the sake of completeness. The material borrowed from other museums includes the following: Western Plethodons from the University of California; Texas P. glutinosus from Bryce C. Brown, Ottys Sanders, John S. Mecham, and the Strecker Museum; P. d. angusticlavius, P. glutinosus, P. ouachitae, and P. caddoensis from the University of Arkansas; P. c. serratus, P. w. wehrlei, and P. w. dixi from the

Chicago Natural History Museum; P. glutinosus, P. w. wehrlei, and P. richmondi from the Carnegie Museum; P. cinereus from the Museum of Comparative Zoology; P. richmondi from the United States National Museum; P. glutinosus and P. j. rabunensis from the Charleston Museum; P. dorsalis from the University of Georgia; P. richmondi and P. glutinosus from the Cincinnati Society of Natural History; P. dorsalis from the Ross Allen-Wilfred T. Neill collection; and the entire Plethodon collection of the Great Smoky Mountains National Park.

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METHODS

The importance of studying living plethodons, because of the usual loss and alteration of their pigments in preservatives, has already been mentioned. It is almost impossible to study geographic variation in pigmentation without considerable field work, and it was initially hoped that this could be done with all the forms in the genus. Unfortunately, several of the forms have not been seen alive and so our knowledge of their geographic variation has not been augmented. However, I have been able to do a considerable amount of field work with some of the Eastern Large Plethodons, and the result has been a considerable amount of new information concerning them. I believe that when similar studies of other species are made, they will be found to vary as much as glutinosus and jordani in pigmentation characters.

A perusal of the literature on this genus will disclose that most workers have given considerable weight to variation in the number of costal grooves. A careful study of the literature indicates, however, that there is not agreement in the reports of number of costal grooves in many species. The reason for this was apparent to the writer when I failed to obtain consistant counts on the same specimens counted at different times. A method for accurately determining the true variation in body segmentation would be a necessary preliminary to the use of this character in studying relationships. Since the costal grooves show a direct correlation with the number of vertebrae, a method of counting the number of trunk vertebrae by the use of X-ray photographs was devised. As an outgrowth of this study, a method for counting costal grooves which will accurately reflect the body segmentation of salamanders of this genus will be reported below.

Many other characters have been used in the study of the systematics of this genus. As far as possible, these have been restudied using much new material that has recently become available. Several nomenclatorial changes will be suggested based on an attempt to best indicate the biological relationships of these organisms.

The results of this study have clearly indicated that there are three major natural subdivisions of the genus Plethodon. These would probably be considered subgenera in most animal groups, but herpetologists have rarely used subgenera in their classification. Although the use of subgenera would be helpful in this case, common names will be used for these groups in conformity with current herpetological practices. They will be referred to as the "Western Pleth-

odons," "Eastern Small Plethodons," and "Eastern Large Plethodons." Each of these subdivisions of the genus is further divided into species groups consisting of species which are more closely related to each other than they are to any other similar group. In a few cases, species which are morphologically quite distinct from any other species in their section of the genus have been segregated into a species group consisting of a single species.

For each taxon, information on the morphology, variation, and distribution is given, followed by a synonomy, data on the type specimen, diagnosis of the form, and a description of the pigmentation, segmentation, number of vomerine teeth, and size. Detailed descriptions of several hundred specimens were made during the course of this study. For most forms, similar data are available in Bishop (1943) or Stebbins (1951) or in the original description. It is unnessary to repeat these here, since the concern is variation of populations, not detailed descriptions of individual specimens.

Dunn (1926) presents fairly complete synonomies for each of the forms known at that time. Therefore the large number of references on the distribution and habits of the more common forms are not included here. An attempt has been made to include the first reference to each combination of names, as well as most of the papers dealing with the systematics of each form. Check lists have usually been omitted, except when new combinations of names or other new information is presented. Consistancy has not been a goal, and some papers dealing with habits or distribution have been included in the synonomies of little known species, while similar papers on well known forms

that do not contribute new information have been omitted.

The locality maps have been prepared mainly as an aid to the discussion of the distribution of the various species groups. They are based on literature records as well as specimens examined by the writer. Maps showing the distribution of many of these forms are available elsewhere, but there have been many changes in the taxonomy since the publication of some of these, and it seems desirable to include them here in spite of the fact that there is some repetition. New information on the geographic distribution of several of the forms is included on some of the maps.

Seventeen subspecies are recognized in this paper. An examination of the distribution maps indicates that several of the polytypic species exhibit terminal raciation and most of these races are isolated from their nearest relatives by areas of uninhabited country. This is true of the races of P. vandykei, P. dorsalis, P. cinereus, and to some extent, P. glutinosus. The subspecies of P. wehrlei are poorly defined, and need more study. There do not appear to be natural barriers between some of the subspecies of P. richmondi and P. jordani, and there is evidence that intermediate populations are present between some of the races. A more detailed consideration of raciation in both of these species is given below.

THE RELATION BETWEEN NUMBER OF COSTAL GROOVES AND TRUNK VERTEBRAE IN PLETHODON

Radiographs of series of specimens of all the species in this genus have indicated that the number of trunk vertebrae in a

single population is remarkably constant. (Since there is little differentiation of the salamander body vertebrae into regions, Francis (1934) suggests that all precaudal vertebrae, except the atlas and the sacrum, be called trunk vertebrae.) There is never a variation of more than three trunk vertebrae in a single population and with few exceptions, the intermediate figure has a very high frequency of occurrence. The value of this character in studying variation becomes apparent when it is found that a difference of a single vertebra between two populations is easily detectable and has been used successfully as a key character to separate a high proportion of specimens of two contrasted forms.

A method of counting costal grooves that would accurately reflect the number of trunk vertebrae would be much more effective in the taxonomic study of this genus. At present, their use is rather limited, since they are rarely counted consistantly by different workers. Pope (1950: 102) correctly summarizes the existing situation by stating that "variation of a magnitude of one or two grooves will be meaningless unless the same worker has made all the counts and done so with great care." The method described here has been found to correctly correspond with the number of trunk vertebrae with over 90% accuracy.

The atlas is not related to any costal grooves. The first trunk vertebra is located just anterior to the gular fold and its rib does not appear to be associated with the gular fold or with any of the costal grooves. The rib of the second trunk vertebra is located in the myoseptum of the first costal groove. The external position of this groove varies somewhat, but is usually close to the front

limb insertion. If the first costal groove is poorly defined or absent, as often occurs when it is located directly over the front limb insertion, it should be counted, as the space obviously corresponds to a vertebra whether the groove is visible or not. The individual variation in the position of the first costal groove is probably due to the variation in the position of the pectoral girdle relative to the vertebrae. The girdle may be located opposite the second trunk vertebra, between the second and third trunk vertebrae, or opposite the third trunk vertebra. The ribs of the third trunk vertebra extend posteriorly so that the second costal groove is always posterior to the front limbs.

There is a one-to-one relation between the remaining body vertebrae and the costal grooves, except in the case of rare aberrations (one vertebra possessing two or more pairs of ribs, or one vertebra possessing a rib on only one side, in which case a corresponding costal groove is present only on that side). The last pre-sacral vertebra (usually the only trunk vertebra which does not possess ribs) is represented by the groove just anterior to the insertion of the hind limbs. Often this groove joins ventrally the one just preceeding it so that on the lower sides there is only onegroove which is forked dorsally. Both grooves should be counted, since they correspond to two separate vertebrae. The groove present over the hind limb insertion (sometimes weakly developed or absent) corresponds to the sacral vertebra, and each groove on the tail corresponds to a caudal vertebra.

There is much more individual variation in the position of the sacral vertebra in relation to the pelvic girdle than there is in the relation of the shoulder girdle to the second and third trunk vertebrae.

The sacral vertebra may be located so far anterior to the pelvic girdle that the first caudal vertebra is opposite the hind limbs. It may also be slightly anterior, opposite, or slightly posterior to the pelvic girdle. Occasionally when it is posterior to the girdle, the costal groove corresponding to the last trunk vertebra is located over the hind limb. This is the major source of error in attempting to accurately correlate the number of costal grooves with the number of trunk vertebrae. Fortunately, however, fewer than 10% of the specimens examined were in this category. Using this method, costal groove counts were made on 85 specimens of several species of the genus Plethodon (including specimens possessing 15 to 22 trunk vertebrae), and 93% of the counts accurately represented the number of trunk vertebrae obtained from X-ray photographs. Since the first trunk vertebra is not associated with a costal groove, the number of costal grooves is always one less than the number of trunk vertebrae. It would therefore appear that this method can be used advantageously to obtain an accurate estimate of the number of trunk vertebrae of all the species of the genus Plethodon.

Occasionally the sacral rib may attach to one vertebra on one side of the animal and to the following vertebra on the other side. Rarely, there are two sacral ribs issuing from two successive vertebrae on the same side of the animal. The suggested method of counting costal grooves is of no value in detecting such abnormalities.

PIGMENTATION IN THE GENUS PLETHODON

Pigmentation in living specimens was studied with the aid of a dissecting microscope. Although there is great variety in the coloration of the animals included in this genus, the actual different types of pigments are few. No histological or biochemical studies of the pigments have been made, thus similarity in the appearance of the pigmentation is the basis for the above statement. Three main types were identified and are called melanophores, guanophores, and lipophores, following Stebbins (1951).

Melanophores are present in all the forms in the genus. They are responsible for the dark ground color of these salamanders. The other pigments generally occur in gaps in the melanophore ground color.

Guanophores are responsible for the white and brassy spots, present on many of the species. There appears to be little difference in the structure of the different colored guanophores, but mainly a difference in the amount and color of light reflected from the spots. The iridescence characteristic of animals with "brassy" "dorsal spots appears to be centered in small round crystalline structures found at intervals along the pseudopodia of the guanophores. The number of these crystals seems to determine the amount of the iridescence that has been variously described by different workers as "brassy flecking," metallic golden spotting," "golden blotches," "bronzy mottling," and "frosting." This type of guanophore pigmentation is present in the iris of most of the Eastern Small Plethodons and the Western Plethodons, and is present on the dorsum of many of the species. It is responsible for the brassy dorsal flecks of glutinosus, ouachitae, dixi, clemsonae, popei, nettingi,

cinereus, polycentratus, dorsalis, welleri, and vehiculum. In welleri, these guanophores are concentrated to form dense clusters. In glutinosus, they are usually associated with other white guanophores. In the other forms they are scattered over the back and are not clumped into spots. Brassy flecks are rarely found other than in the iris or on the dorsum of salamanders of this genus.

Guanophores that lack the brassy iridescence are common on the belly and sides of many species, and are also present on the dorsum, occasionally occurring there with the brassy type. They have a much greater tendency to be clumped together to form larger spots than do the brassy flecks, but are occasionally found singly. In glutinosus, for example, it is often possible to see, on the same animal, every type of intermediate between the brassy type and those which lack the brassy iridescence.

The white guanophores are characteristically found on the dorsum of glutinosus, ouachitae, cinereus, polycentratus, popei, dorsalis, and vehiculum. They are present on the sides of almost all of the eastern species (except metcalfi and melaventris), and on the bellies of all the Eastern Small Plethodons. Often these lateral and ventral spots have a yellowish color, but this is not due to the presence of brassy flecks.

Lipophores do not have the structure of guanophores in that they lack the pseudopodia which can easily be observed in the guanophores. The red color of jordani, shermani, wehrlei, yonahlossee, ouachitae, cinereus, polycentratus, serratus, dorsalis, and vehiculum

appears to be due to the same type of lipophore pigment. The dorsal band of yonahlossee is a darker color because of the additional presence of melanophore pigment. Lipophores may also be yellow in color, as in some cinereus, vehiculum, and dunni.

The variety of colors present in the genus seems to be due entirely to variation in the abundance of these pigments or various combinations of the three. In some forms, the lipophores or guanophores or both are lacking. There is also variation in the concentration of melanophores. These pigmentation characters may vary somewhat within a species, both individually and geographically, but are fairly uniform in most forms, enabling a person familiar with living specimens to easily identify most salamanders by the color pattern alone. The phylogenetic significance of the distribution of these pigments in the various plethodons is discussed below in the accounts of the various forms.

KEY TO THE SALAMANDERS OF THE GENUS PLETHODON

The key is based mainly on the average number of trunk vertebrae occurring in each of the forms. Before using this key, it is suggested that the section on the method of counting costal grooves that accurately reflects the number of trunk vertebrae be read. A small percentage of specimens of each form may not be correctly identified on this basis, but a small series will usually key out correctly. Ranges are included and locality data may proove more helpful in identifying preserved specimens than pigmentation characters.

1 a Costal grooves usually 14 2

b Costal grooves 15 or more 4

2 a Ventral color reddish (Multnomah County, Oregon, and Skamania County, Washington) . . . . . P. v. larselli

b Ventral color not reddish 3

3 a Yellow or orange dorsal stripe contrasts sharply with the lateral black ground color; the proximal segments of the limbs dark in color (Kootenai County, Idaho) P. v. idahoensis

b Ground color light, not contrasting sharply with the dorsal stripe; yellow lipophore pigment similar to that found on the dorsum present on the proximal segment of the limbs (western Washington) . . . . . P. v. vandykei

4 a Costal grooves usually 15 (western Oregon and southwestern Washington) . . . . . P. dunni

b Costal grooves 16 or more 5

5 a Costal grooves usually 16 6

b Costal grooves 17 or more 20

6 a Belly mottled with yellow or red, white and black; size small, usually under 50 mm. snout-vent length; often a red, tan, or yellow dorsal stripe (southwestern British Columbia, including Vancouver Island, western Washington and western Oregon) . . . . . P. vehiculum

b Belly usually dark, at least posteriorly, or with scattered small white ventral spots; size usually larger (except welleri and caddoensis); dorsal stripe usually absent (except yonahlossee and ouachitae) (eastern United States) 7

7 a Red pigment present on back, legs, or cheeks 8

b No red pigment present on animal 11

8 a Red pigment confined to sides of head or legs in adults . 9

b Red pigment largely restricted to dorsum 10

9 a Red pigment most abundant on sides of head (Great Smoky Mountains of Tennessee and North Carolina) . . *P. j. jordani*

b Red pigment most abundant on legs (Nantahala Mountains, North Carolina) . . . . . *P. j. shermani*

10 a White pigment lacking in dorsal stripe (Blue Ridge Mountains of southwestern Virginia, northeastern Tennessee, and northwestern North Carolina) . . . . . *P. yonahlossee*

b Abundant white pigment occurring within the dorsal stripe (Ouachita Mountains of Arkansas and Oklahoma) . *P. ouachitae*

11 a Size small, adults not over 50 mm. snout-vent length; back with large coalescing iridescent brassy spots, usually covering about half the area of the dorsum (Blue Ridge Province of southwestern Virginia, northeastern Tennessee and northwestern North Carolina) *P. welleri*

b Back without dorsal brassy spots, or if present, they are small in size and cover less than one quarter of the area of the dorsum 12

12 a Body entirely black, guanophores and lipophores absent . . 13

b Dorsum and/or sides with guanophore spotting 14

13 a Belly much lighter than dorsum (mountains of western North Carolina and adjacent Tennessee and Virginia) *P. j. metcalfi*

b Belly almost as dark as dorsum (southwestern North Carolina) . . . . . *P. j. melaventris*

14 a Back with large conspicuous white or brassy dorsal spots . 15

b Back without large conspicuous guanophore spotting, or if present, the spots are of very small size 17

15 a Melanophore pigmentation on chin greatly reduced, compared to belly 16

b Melanophore pigmentation on chin similar to that on belly (eastern United States from southern New York to northern Florida, west to eastern Louisiana, Illinois, Missouri, eastern Oklahoma, and the Balcones Escarpment in Texas) . . . . . P. g. glutinosus

16 a Dorsum with white spots only (Balcones Escarpment in east central Texas) . . . . . P. g. albagula

b Dorsum with large white spots and smaller brassy flecks (Caddo Mountains of Arkansas) . . . . . P. caddoensis

17 a Dorsum with very small white or brassy spots 18

b Dorsum black, without any guanophore spotting 19

18 a Dorsum covered with tiny brassy flecks (vicinity of Jocassee, South Carolina) . . . . . P. j. clemsonae

b Dorsum with very tiny scattered white spots (Tusquitee and Snowbird Mountains of western North Carolina) . . . . . P. j. teyahalee

19 a Belly much lighter than ground color of back (Unicoi Mountains of western North Carolina and eastern Tennessee) . . . . . P. j. unicoi

b Belly nearly as dark as dorsal ground color (mountains of northeastern Georgia . . . . . P. j. rabunensis

20 a Costal grooves usually 17 21

b Costal grooves 18 or more 23

21 a Large red spots on dorsum of adult (southwestern Virginia) . . . . . *P. w. jacksoni*

b Red spots absent from dorsum of adult 22

22 a Dorsum with numerous white and brassy spots (Roanoke County, Virginia) . . . . . *P. w. dixi*

b Dorsum with very small white or brassy spots (Cattaraugus County, New York, south through western Pennsylvania, adjacent Ohio, and West Virginia) . . . . . *P. w. wehrlei*

23 a Costal grooves usually 18 24

b Costal grooves 19 or more 27

24 a Size large, up to 66 mm. snout-vent length (northwestern California and southwestern Oregon) . . . . . *P. productus*

b Size small, up to 45 mm. in snout-vent length (eastern United States) 25

25 a Belly mottled with red, yellow, white, and black pigment . 26

b Belly black, with small white spots (Cheat Mountains of West Virginia) . . . . . *P. r. nettingi*

26 a Dorsal stripe very narrow, less than 1/3 the width of the body (southwestern Missouri, northwestern Arkansas, and adjacent Oklahoma) . . . . . *P. d. angusticlavius*

b Dorsal stripe much wider than 1/2 the width of the body, edges of stripe very irregular (southern Illinois, Indiana, and southern Ohio, south through Kentucky and Tennessee to northern Alabama and northwestern Georgia) . *P. d. dorsalis*

27 a Costal grooves usually 19 28

b Costal grooves 20 or more 30

28 a Fifth toe on hind foot usually with one phalanx (Jemez Mountains of New Mexico) . . . . . P. neomexicanus

b Fifth toe on hind foot with two phalanges (eastern North America) 29

29 a Dorsal red stripe with straight edges (southern Canada, south to North Carolina, eastern Kentucky, southern Illinois, and eastern Missouri) . . . . . P. c. cinereus

b Dorsal red stripe with serrations corresponding to each costal groove (western Arkansas and eastern Oklahoma) . . . . . P. c. serratus

30 a Red pigment present on sides and dorsum (northwestern Georgia) . . . . . P. c. polycentratus

b No red pigment on animal 31

31 a Costal grooves usually 21 or more (western Pennsylvania, southern Ohio, eastern Kentucky, south to northwestern Virginia) . . . . . P. r. richmondi

b Costal grooves usually 20 (southwestern Virginia, northwestern North Carolina, and adjacent Kentucky) . P. r. popei

SYSTEMATICS

Plethodon Tschudi

Plethodon Tschudi (1838: 58). Genotype (by original designation): Salamandra glutinosa Green.

Phatnomatorhina Bibron in Bonaparte (1839). (Substitute name)

Sauropsis Fitzinger (1843: 33). (non Sauropsis Agassiz, 1832, Jahrb. Min., 3: 142). Genotype (by original designation): Salamandra erythronota Green.

Diagnosis:- Plethodontidae with tongue attached in front; premaxillae separate; teeth on posterior portion of maxillae; tail not constricted at base; five toes on the hind feet; no palmar tubercles; terminal phalanges normal; and no aquatic larval stage.

According to Dunn (1926), the closest relatives of Plethodon are Batrachoseps, Ensatina, Aneides, and Hemidactylium. All four of these genera differ from Plethodon in several fundemental characteristics. Batrachoseps and Hemidactylium possess only four toes on the hind feet. Ensatina and Hemidactylium possess a basal constriction of the tail. Ensatina has palmar tubercles. The premaxillae are fused in Aneides and Batrachoseps (except B. wrighti). Hemidactylium has an aquatic larval stage. Aneides lacks teeth on the posterior portion of the maxilla and has expanded terminal phalanges. Dunn (1926: 22) believed that Plethodon is the most primitive genus in this group of genera and that the others, with the possible exception of Ensatina, are more specialized than Plethodon. The genus Plethodon is the largest in number of species, and there is more divergence within the genus than in the other related genera. This might be considered evidence for, but not necessarily proof of, a greater age for this genus.

Grobman (1944: 266) suggests that the relationship between the Eastern Large and Small Plethodons is not close and lists size and costal groove differences which distinguish them. Actually there is some overlap between the Eastern Large and Small Plethodons in these characters, but there are other important differences between the two groups. The mental gland is much better developed in male Eastern Large Plethodons than in the Eastern Small Plethodons. The worm-like body and shorter legs of the Eastern Small Plethodons is characteristic. The Eastern Small Plethodons have fewer teeth and there is a great deal of variation in the number of trunk vertebrae within the group (range 16-24), whereas the Eastern Large Plethodons show very little variation (range 16-19). There is more webbing on the toes of the small forms than in the large species. The Eastern Large Plethodons have an unpigmented parietal peritoneum, while in the small species the peritoneum is pigmented with melanophores. The differences in the structure of the vertebrae are discussed below.

One species, P. wehrlei, is usually included with the Eastern Large Plethodons on the basis of size, but in several ways it is intermediate between the two groups. It has more costal grooves and fewer teeth than other Eastern Large Plethodons. Its toes are webbed as in the Eastern Small Plethodons and the peritoneum has a few melanophores. Were it not for the intermediate character of this species, the two groups should probably be recognized as distinct genera, but the somewhat intermediate nature of wehrlei would seem to indicate that they have not become sufficiently distinct to justify such an action. The two groups could best be regarded as subgenera, but to conform with current practise, the common names, Eastern Large Plethodons and Eastern

Small Plethodons, will be used in this paper. Although P. wehrlei possesses more characters that would link it with the Eastern Small Plethodons than do any of the other Eastern Large Plethodons, it is probably more closely related to members of the latter group. Therefore, it is included as a separate species group under the Eastern Large Plethodons. Its intermediate position is important, however, in linking the two groups.

During studies on the osteology of this genus, certain differences in the vertebrae of the two eastern sections of the genus have been noted. The height of the vertebrae of the Eastern Small Plethodons is proportionately less and the vertebrae usually lack the neural spines that are present on those of the large eastern species (see figure 1). P. wehrlei is not intermediate in this regard, but closely resembles the other Eastern Large Plethodons. The vertebrae of all the eastern species have been examined except for caddoensis and richmondi.

To investigate the relationship of the western forms with those in eastern North America, each of the above differential characters was studied in all five of the western species. As with the eastern forms, the size varies within the group, but four of the five western species are as large as most of the Eastern Large Plethodons. The number of trunk vertebrae varies considerably in the western forms (range 15-20). The mental gland is poorly developed in all the Western Plethodons. The body form is variable, ranging from short and stout in vandykei to very elongate in neomexicanus. The number of vomerine teeth is low in the western forms. The toes of two species (dunni and vehi-

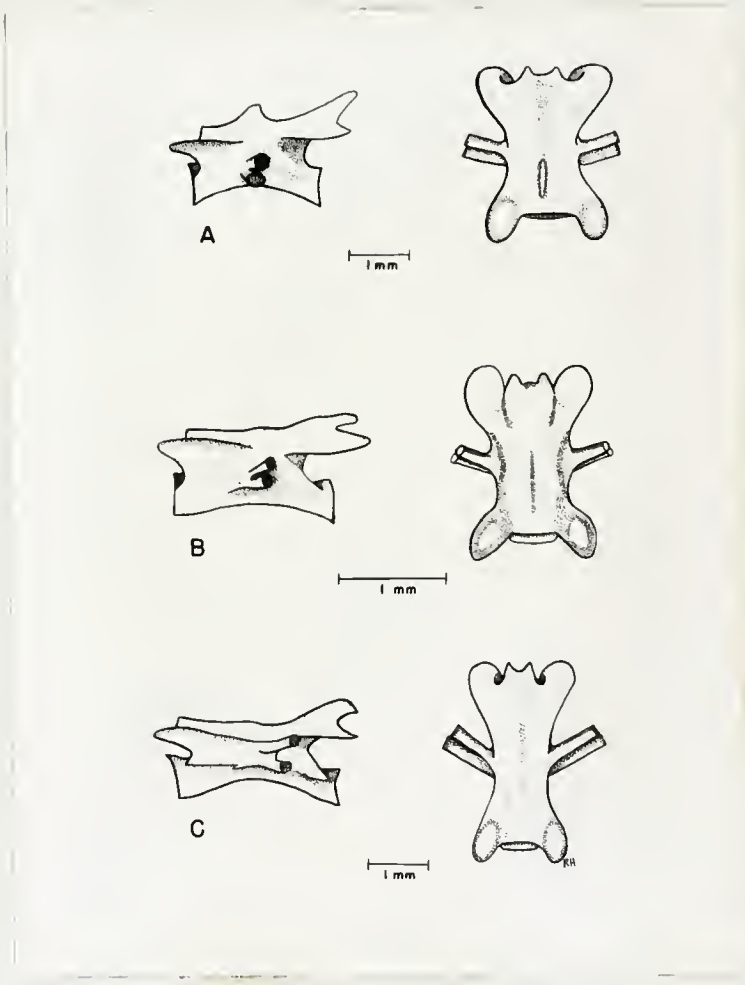

Figure 1. Lateral and dorsal views of the trunk vertebrae of representatives of the three major groups of the genus Plethodon. A. P. glutinosus. B. P. welleri C. P. dunni

culum) are very slightly webbed, while the other three species have webbed toes. The peritoneum of all of the Western Plethodons is pigmented with melanophores. The vertebrae of the western forms are quite different from both eastern types (P. neomexicanus has not been examined). They are proportionately longer and have longer transverse processes than any of the eastern species. As a group, the Western Plethodons are more variable, and in at least one character, the structure of the vertebrae, they are very distinct from both eastern sections of the genus. It would appear that the Western and Eastern Plethodons have been separated for a long time, and that both have undergone considerable speciation during this period.

In several ways, the Eastern Small Plethodons resemble the Western Plethodons more closely than do the Eastern Large Plethodons. The red or yellow dorsal stripe is more common in both groups than it is in the Eastern Large Plethodons. Both have a great amount of variation in the number of trunk vertebrae and degree of elongation of the body. Both have low vomerine teeth counts and a pigmented peritoneum. Both have a less well developed mental gland than the Eastern Large Plethodons (except for dorsalis). It would appear that the Eastern Large Plethodons are the more specialized forms, with a larger number of vomerine teeth, loss of pigmentation in the peritoneum, and increase in the development of the mental gland. The fact that P. wehrlei possesses characteristics of both groups would indicate that both were derived from a common ancestor. This common ancestor was probably more like the Eastern Small Plethodons and the Western Plethodons in most of its characteristics, since it would be unlikely that these two groups would have independently converged toward each other

in so many ways from an ancestor that was similar to the Eastern Large Plethodons as suggested by Dunn. The relationships of the three groups would appear to be best indicated by a phylogeny similar to that shown in figure 2.

The relationship of the Western Plethodons with the other plethodontid genera in western North America needs further study. It may be that the Western Plethodons are more closely related to Batrachoseps, Ensatina, or western Aneides than they are to any of the Eastern Plethodons. The western plethodontid salamanders may have been isolated from their eastern relatives for a long period of time. The fact that two groups now included in the genus Plethodon, one in eastern North America and the other in the western part of the continent, have both retained many primitive characteristics, does not necessarily mean that they are still generically related to one another. The fact that each of these groups (the Western and Eastern Plethodons) has more species than any other plethodontid genus in its region, as well as the the fact that these species are so diverse, would suppot the view that they have been separated for a long period of time. A review of this entire problem is needed, but it would involve an investigation of the characteristics of the genera Aneides, Batrachoseps, Ensatina, and Hemidactylium, and is beyond the scope of this study. Such an inquiry should be completed before erecting a new genus for the Western Plethodons, but this arrangement seems to be indicated by the present incomplete information.

The systematic arrangement of the genus Plethodon suggested in this paper is as follows:

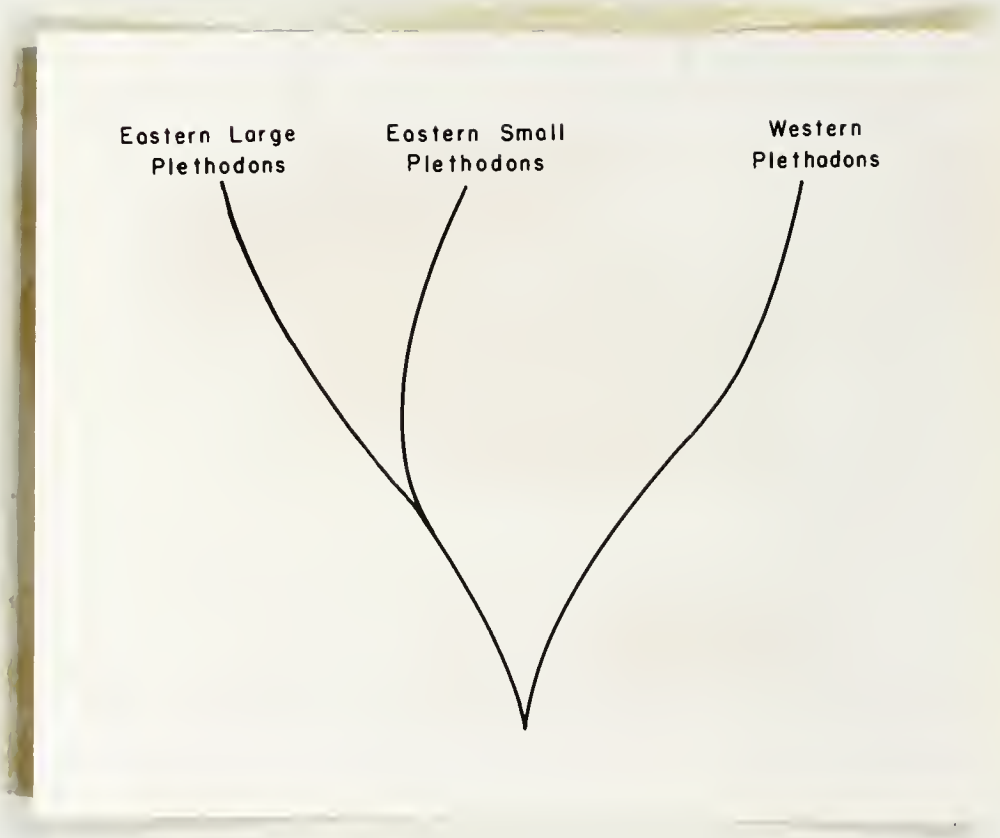

Figure 2. Suggested phylogeny of the major subdivisions of the genus Plethodon.

Western Plethodons

Plethodon vandykei Group

Plethodon vandykei vandykei Van Denburgh

Plethodon vandykei idahoensis Slater and Slipp

Plethodon vandykei larselli Burns

Plethodon vehiculum Group

Plethodon dunni Bishop

Plethodon vehiculum (Cooper)

Plethodon productus Group

Plethodon productus new name

Plethodon neomexicanus Group

Plethodon neomexicanus Stebbins and Riemer

Eastern Small Plethodons

Plethodon welleri Group

Plethodon welleri alker

Plethodon richmondi richmondi Netting and Mittleman

Plethodon richmondi popei Highton and Grobman

Plethodon richmondi nettingi Green

Plethodon cinereus Group

Plethodon dorsalis dorsalis Cope

Plethodon dorsalis angusticlavius Grobman

Plethodon cinereus cinereus (Green)

Plethodon cinereus serratus Grobman

Plethodon cinereus polycentratus Highton and Grobman

Eastern Large Plethodons

Plethodon wehrlei Group

Plethodon wehrlei wehrlei Fowler and Dunn

Plethodon wehrlei dixi Pope and Fowler

Plethodon wehrlei jacksoni Newman

Plethodon yonahlossee Group

Plethodon yonahlossee Dunn

Plethodon ouachitae Dunn and Heinze

Plethodon caddoensis Pope and Pope

Plethodon glutinosus Group

Plethodon jordani jordani Blatchley

Plethodon jordani metcalfi Brimley

Plethodon jordani shermani Stejneger

Plethodon jordani unicoi new subspecies

Plethodon jordani melaventris Pope and Hairston

Plethodon jordani rabunensis Pope and Hariston

Plethodon jordani teyahalee Hairston

Plethodon jordani clemsonae Brimley

Plethodon glutinosus glutinosus (Green)

Plethodon glutinosus albagula Grobman

The Western Plethodons

The Western Plethodons include five species, none of which, except for dunni and vehiculum, appear to have close affinities. P. vandykei, with three presently recognized subspecies, vandykei, larselli, and idahoensis, occurs in coastal Washington, northwestern Oregon, and northern Idaho. P. dunni is known from southwestern Washington and coastal Oregon. P. vehiculum ranges on the coast from central Oregon to southern British Columbia, including Vancouver Island. P. productus (formerly P. elongatus) occurs in a small area in northwestern California and southwestern Oregon. P. neomexicanus is known only from the Jemez Mountains of New Mexico.

Stebbins (1951) has recently summarized the knowledge of the amphibians of western North America, and has given detailed descriptions of all five species in life. Little new information on individual or geographic variation can be offered here since I have had no field experience with these animals and only four forms (idahoensis, dunni, vehiculum, and productus) have been examined in life. Reference should be made to Stebbins' book for further information on these forms.

Radiographs of a series of each of the forms (except the recently described P. v. larselli) were taken and the number of trunk vertebrae in each form is shown in table I. The usual number of trunk vertebrae in each species of Western Plethodon is different, and none of the known forms possess 18 trunk vertebrae as the modal number.

Except for vehiculum, all of the Western Plethodons are fairly large in size. All but neomexicanus possess a stripe phase in the adult, and all but dunni and vehiculum have webbed toes. The vomerine tooth

TABLE I

THE NUMBER OF TRUNK VERTEBRAE IN WESTERN FORMS OF THE GENUS PLETHODON

Form	Number of trunk vertebrae					
	15	16	17	18	19	20
P. v. vandykei	3					
P. v. idahoensis	11	4				
P. dunni		27	1			
P. vehiculum		10	32	7		
P. productus				1	15	2
P. neomexicanus						7

counts of all of the western forms are low compared to Eastern Large Plethodons of similar size; vehiculum and productus have especially low vomerine counts.

P. vandykei is unusual in possessing a parotid gland and in having the lowest number of vertebrae in the genus. P. neomexicanus is unusual in being the only species in the genus that has a reduced fifth toe on the hind limbs.

Plethodon dunni and Plethodon vehiculum appear to be rather closely related. P. dunni attains a larger size than P. vehiculum and has more vomerine teeth. P. vehiculum usually has one more trunk vertebra than dunni. P. dunni has more aquatic habits than vehiculum. The color of the dorsal lipophores in the striped phase of the two forms is different. The stripe of dunni is usually greenish yellow, while that of vehiculum varies from reddish tan to yellow. The toes are very slightly webbed in both and most other structural features are similar.

The other Western Plethodons possess a considerable amount of webbing on their toes. The amount of webbing on the toes does not appear to be correlated with aquatic tendencies, since the two most aquatic forms, dunni and vandykei, represent extremes in the absence and presence of webbing in the western forms. The forms vehiculum and productus, both with more terrestrial tendencies, also differ greatly in amount of webbing between the toes. Moreover, in the eastern United States, some of the forms have webbed toes, while others do not, yet all are terrestrial.

There is no doubt that dunni and vehiculum should be regarded

as distinct species, since the two occur sympatrically through most of the range of dunni without any evidence of interbreeding. A study of this relationship and the possible differences in the habitat niches of the two forms, suggested by Stebbins (1951: 65), is much to be desired.

The forms, vandykei, productus, and neomexicanus all seem to differ from each other as much or more than species groups in the Eastern Plethodons. The fact that they are so distinct morphologically makes it difficult to determine their relationships. In all probability, these forms have been differentiating for a long period of time. There has probably been a considerable amount of extinction of humid forest dwelling western North American amphibians due to climatic changes which have occurred during or since the Tertiary. The present discontinuous distribution of this genus in the area, with only two species recorded in the Rocky Mountains, separated by almost a thousand miles, supports this view. Without doubt there are probably other undiscovered forms of this genus in the western United States. Many salamanders of the region are difficult to collect, except during extremely favorable conditions, and some may have been overlooked in spite of intensive collecting. There remain many areas in which there has been very little collecting, and these may be profitably searched for members of this genus. Lowe (1955: 250), for example, believes that plethodontid salamanders will be found in the higher mountains of Arizona because conditions there are similar to those where they have been taken in other areas.

The relationships of these salamanders would seem to be best indicated by the phylogeny shown in figure 3.

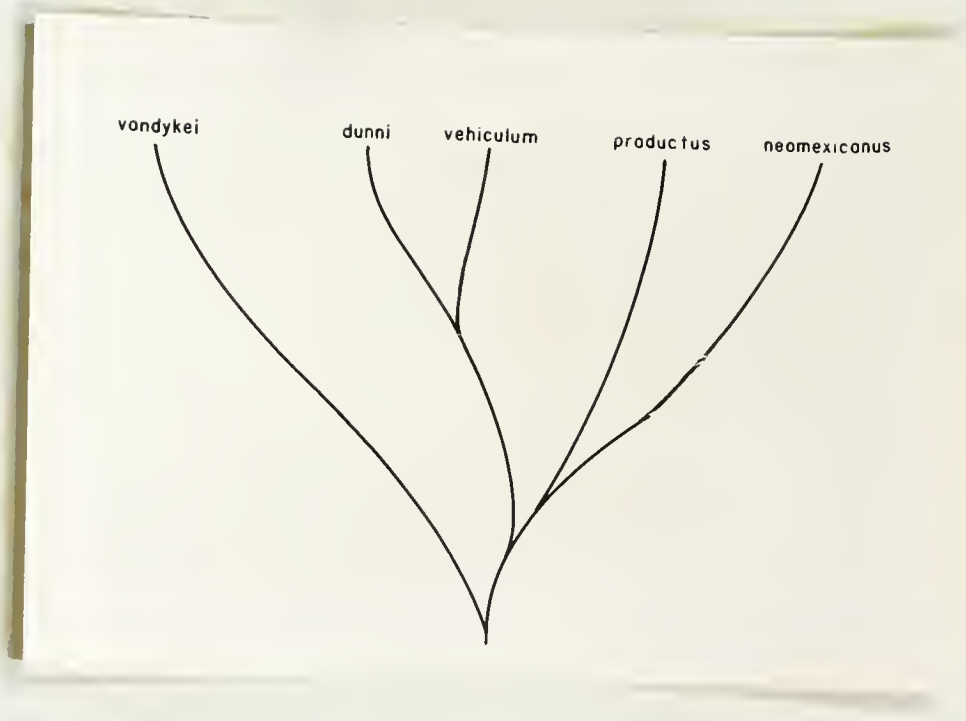

Figure 3. Suggested phylogeny of the Western Plethodons.

Plethodon vandykei Group

Plethodon vandykei

This species is known from the Coast Range, Olympic Mountains, and Cascade Mountains of western Washington; Coeur d'Alene Lake, in northern Idaho; and from Larch Mountain, Multnomah County, Oregon. The Idaho population was described as a distinct species (idahoensis) by Slater and Slipp (1940: 38), but has been considered a subspecies of vandykei by Lowe (1950: 93) and more recent workers. Although the Idaho and Washington populations of this species are usually believed to be isolated from one another, Savage (1952: 183) suggests that they may be connected by a corridor of high humid country along the international boundary between Washington and British Columbia. The two forms, idahoensis and vandykei, apparently differ mainly in color characters.

In 1954, Burns discovered Plethodon vandykei in Multnomah County, Oregon. Two specimens from Larch Mountain were unusual in possessing red bellies. A series of eleven specimens collected on the north side of the Columbia River, at Archer Falls, Skamania County, Washington, also agreed in coloration with the Oregon specimens and this red-bellied form was described as the third subspecies of vandykei, P. v. larselli.

Stebbins (1951: 80-1) states that there are two color phases of P. v. vandykei. The light phase has the color of the belly and sides very similar to that of the dorsal stripe, while the dark phase has a darker lateral and ventral pigmentation.

This species is usually found in very damp situations and thus replaces P. dunni ecologically, as well as geographically. It has re-

cently been shown that their ranges do overlap slightly in Multnomah County, Oregon (Burns, 1954: 85) and Pacific County, Washington (Storm, 1955: 64-5).

Plethodon vandykei vandykei Van Denburgh

Plethodon vandykei Van Denburgh (1906: 61). Dunn (1926: 151-3). Slater (1933: 44). Bishop (1943: 275-8). Storm (1955: 64-5).

Plethodon vandykei vandykei Van Denburgh. Lowe (1950: 93). Stebbins (1951: 80-4). Stebbins (1954: 56-7). Slater (1955: 132-3).

Type:- CAS 6910 (now destroyed), collected at Paradise Valley, Mount Ranier National Park, Washington, by E. C. Van Dyke, in July, 1905.

Diagnosis:- A Western Plethodon with 15 trunk vertebrae. It differs from idahoensis in having a wider dorsal stripe, lighter ground color, and by presence of yellow pigment like that found on the dorsum on the proximal segment of the limbs.

Range:- Known from western Washington, from Clallam County south to Pacific County and east to Pierce County (see figure 4).

Description:- This subspecies has not been seen in life and only four preserved specimens were examined. Stebbins (1951: 80-1) gives detailed color notes on this form.

Costal grooves usually number 14 and the trunk vertebrae 15. In the available specimens, vomerine teeth range from 7 to 10 in a series. The largest individual is 56 mm. in snout-vent length.

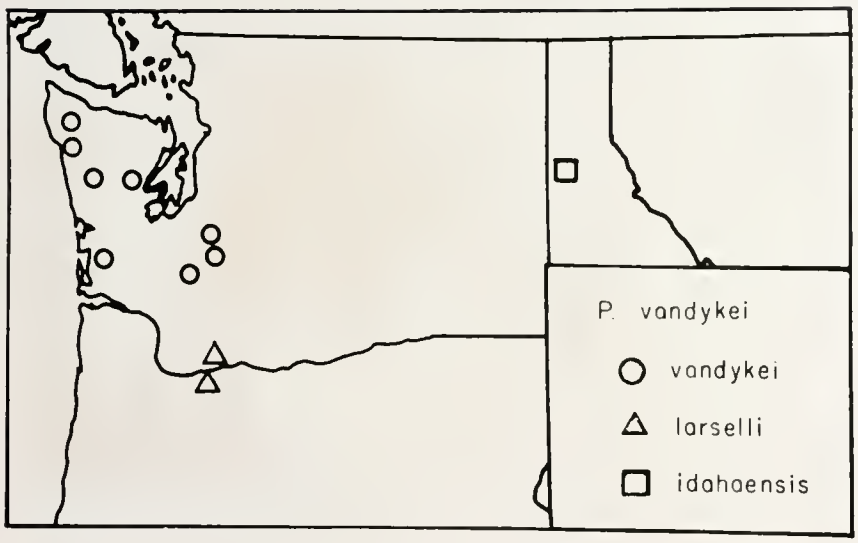

Figure 4. The distribution of the subspecies of Plethodon vandykei in Washington, Oregon, and Idaho.

Plethodon vandykei idahoensis Slater and Slipp

Plethodon idahoensis Slater and Slipp (1940: 38). Slater (1941: 81, 85, 103). Bishop (1943: 259-61). Hilton (1948: 120).

Plethodon vandykei idahoensis Slater and Slipp. Lowe (1950: 93). Stebbins (1951: 80-4). Stebbins (1954: 56-7).

Type:- USNM 110504, an adult male, collected at the northeast corner of Coeur d'Alene Lake, Kootenai County, Idaho, at an elevation of 2160 feet, by James R. Slater, on September 13, 1939.

Diagnosis:- A race of Plethodon vandykei in which the yellow or orange dorsal stripe is narrower than in P. v. vandykei and contrasts sharply with the lateral black ground color, and the proximal segments of the limbs are dark in color.

Range:- Known only from the type locality in northern Idaho (figure 4).

Description:- The back has a dorsal orange or yellow lipophore stripe. The rest of the animal is pigmented with melanophores, except for melanophore gaps on the chin where there are yellow lipophores. There are also brassy guanophores in the iris, and a few scattered white guanophores on the belly and sides.

The costal grooves usually number 14, the trunk vertebrae 15. Vomerine teeth range from 5 to 12 in a series. Of 15 specimens examined, the largest is 56 mm. in snout-vent length.

Plethodon vandykei larselli Burns

Plethodon vandykei larselli Burns (1954: 83-7).

Type:- USNM 134129, an adult male, collected on the north slope of Larch Mountain, three miles from the summit on the Multnomah Falls Trail, Multnomah County, Oregon, on May 24, 1953, by Douglas M. Burns.

Diagnosis:- A race of Plethodon vandykei in which the ventral color is cardinal red to reddish orange.

Range:- Known only from the type locality and from Archer Falls, Skamania County, Washington (figure 4).

Description:- Specimens of this subspecies have not been examined and reference should be made to the original description for details of structure and coloration.

Plethodon vehiculum Group

Plethodon dunni Bishop

Plethodon dunni Bishop (1934: 169). Jewett (1936: 71). Fitch (1936: 637-8). Graf, Jewett, and Gordon (1939: 102). Gordon (1939: 55-6). Slater (1939: 154). Bishop (1943: 242-6). Stebbins (1951: 68-72). Stebbins (1954: 54-5). Storm (1955: 64-5). Dumas (1955: 65). Slater (1955: 132).

Type:- USNM 95196, an adult female, collected just outside the city limits of Portland, Clackamas County, Oregon, by Stanley G. Jewett, Jr., on January 13, 1934.

Diagnosis:- A Western Plethodon with 16 trunk vertebrae.

Range:- Curry County, in southeastern Oregon, north to Pacific County,

Washington, east to the western slope of the Cascade Mountains (figure 5).

Description:- The dorsal stripe is made up of yellowish green lipophores. This pigment also occurs in abundance on the sides, but is reduced on the belly. On the lower sides and belly there are a few yellowish guanophores. There are brassy guanophores in the iris.

The costal grooves usually number 15, the trunk vertebrae 16. The medial end of the vomerine series projects posteriorly toward the parasphenoid patches, so that the two vomerine series form a V. Vomerine teeth range from 4 to 13 in a series. The largest specimen examined is 65 mm. in snout-vent length.

P. dunni is closely related to P. vehiculum, but differs in size, coloration, number of vomerine teeth and number of body segments. It occurs from southwestern Washington south through coastal Oregon. This species occurs sympatrically with P. vandykei in southwestern Washington, with P. productus in southwestern Oregon, and with P. vehiculum throughout most of its range.

P. dunni is apparently the most aquatic Plethodon. Stebbins (1951: 70) states that it is almost invariably found in places that are saturated with water, and that it will often take to the water in an attempt to escape capture.

Most individuals possess a dorsal stripe that is greenish yellow in color, but Stebbins (1951: 69) reports that melanistic specimens lacking the dorsal stripe have been found in Benton County, Oregon.

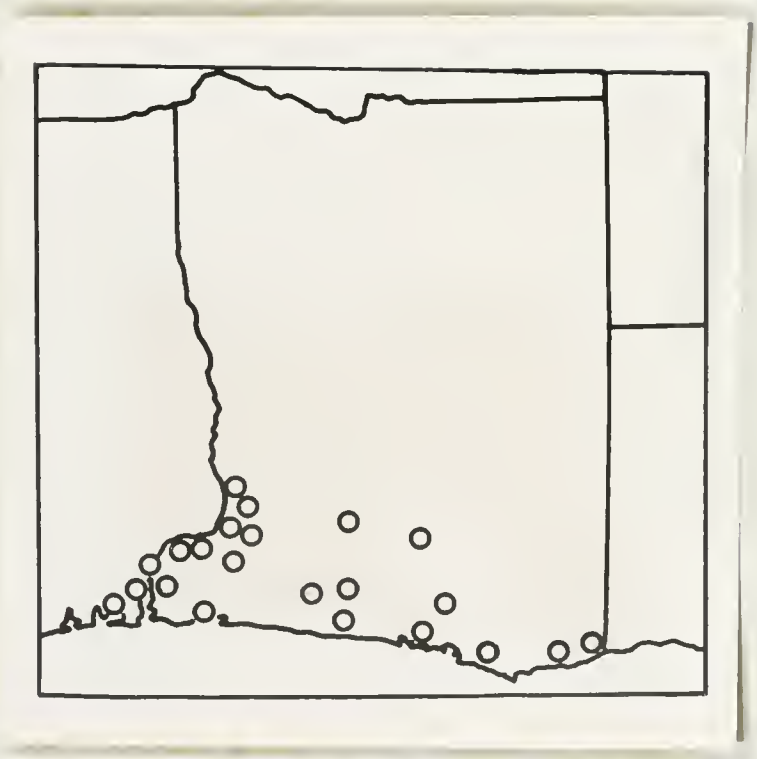

Figure 5. The distribution of Plethodon dunni in Oregon and southwestern Washington.

Plethodon vehiculum (Cooper)

Ambystoma vehiculum Cooper (1860: pl. 31, fig. 4).

Plethodon intermedius Baird (in Cope, 1867: 209). Cope (1869: 100). Strauch (1870: 72). Boulenger (1882: 57). Cope (1883: 23). Garman (1884: 38). Cope (1889: 145-7). Cox (1907: 52). Van Denburgh (1916: 218-9). Fowler and Dunn (1917: 25). Hardy (1926: 22). Kermode (1926: 35). Dunn (1926: 154-6). Slevin (1928: 52-5). Logier (1932: 317-8). Slater (1933: 44). Svihla (1933: 39). Slater (1934: 140-1). Slevin (1934: 46). Cowan (1937: 18).

Plethodon vehiculus (Cooper). Bishop (1934: 171). Jewett (1936: 71). Watney (1938: 89). Slater (1939: 154). Graf, Jewett, and Gordon (1939: 10-1). Brown and Slater (1939: 9).

Plethodon vehiculum (Cooper). Slater (1940: 43). Slater and Brown (1941: 75-7). Bishop (1943: 278-81). Stebbins (1951: 84-7). Stebbins (1954: 57-9). Logier and Toner (1955: 17). Slater (1955: 133-4).

Type:- Apparently no longer in existance. The type locality is Astoria, Oregon.

Diagnosis:- A Western Plethodon with 17 trunk vertebrae.

Range:- From Coos County, in southwestern Oregon, north to southwestern British Columbia, including Vancouver Island (figure 6).

Description:- Lipophores in the region of the dorsal stripe may be absent, producing a uniformly colored phase, or present, resulting in a

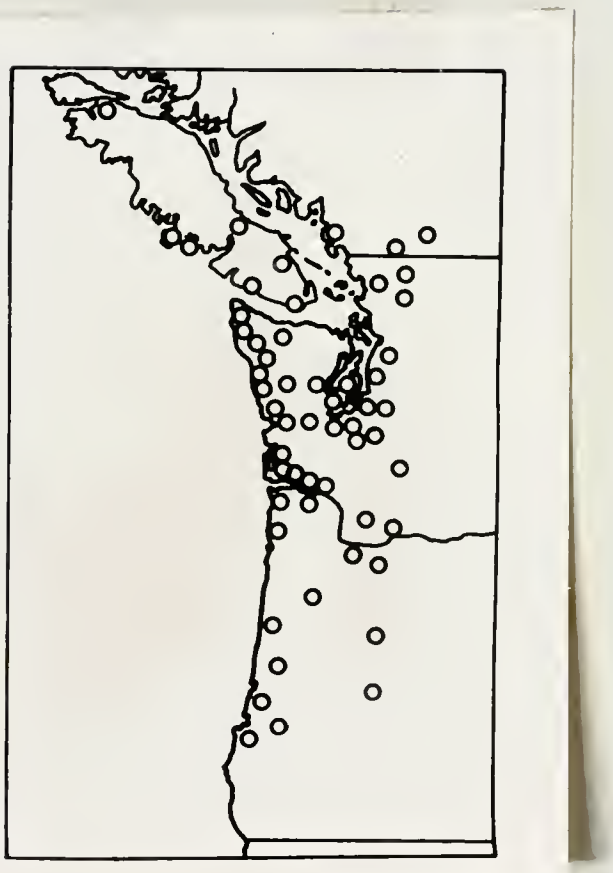

Figure 6. The distribution of Plethodon vehiculum in Oregon, Washington, and British Columbia.

striped phase. The color of the dorsal stripe is quite variable, varying from light yellow, through yellow, orange, and red to brown. The lipophores are absent from the sides, but are present on the belly. The sides are black with only a few small white guanophore spots. These are also present on the belly, and along with the melanophore and lipophore pigmentation give it a mottled appearance. Small white guanophore spots similar to those on the sides, as well as smaller brassy flecks, are present on the dorsum of the dark phase individuals. Brassy guanophores are present in the iris.

Costal grooves usually number 16, trunk vertebrae 17. Vomerine teeth range from 3 to 7 in a series and the two series converge posteriorly to form a V as in dunni. The largest specimen 49 examined is 51 mm. in snout-vent length.

This species is the smallest Western Plethodon and has the largest range. It is the most abundant Plethodon over most of its range. P. vehiculum is superficially quite similar in appearance to the eastern P. cinereus. Dark and striped phases are present and the belly is mottled in both species. The similarities between the two are probably due to convergence or parallel evolution because in all other characters, P. vehiculum is morphologically more similar to the other Western Plethodons.

Plethodon productus Group

Plethodon productus, new name

Plethodon elongatus Van Denburgh (1916: 216-8). (non) Salamandra elongata Valenciennes in Dumeril and Bibron (1854: 84). Grinnell and

Camp (1917: 134). Storer (1925: 21, 104). Dunn (1926: 156-8). Slevin (1928: 55-7). Slevin (1934: 46-53). Wood (1934: 191). Fitch (1936: 638). Wood (1939: 110). Gordon (1939: 13, 30, 56). Bishop (1943: 246-9). Hilton (1946: 45). Stebbins and Reynolds (1947: 41-2). Stebbins (1951: 72-6). Stebbins (1954: 55-6).

Type:- CAS 29096, collected at Requa, Del Norte County, California, by J. R. Slevin, May 22-26, 1911.

Diagnosis:- A Western Plethodon with 19 trunk vertebrae.

Range:- Southwestern Oregon and northwestern California (figure 7).

Description:- The belly of this species is very dark with a few sacttered white guanophore spots. The orange to reddish brown dorsal lipophore stripe is usually brighter in juveniles than in adults, where it is often reduced or absent. Often it is divided into a right and left dorsolateral stripe by the presence of medial melanophore pigment.

The costal grooves usually number 18, the trunk vertebrae 19. Vomerine teeth range from 4 to 7 in a series. This is a large species, the largest of 18 specimens examined is 66 mm. in snout-vent length.

This is the most elongate of the Western Plethodons in the Pacific Northwest. Its greater number of body segments distinguishes it from the species vandykei, dunni, and vehiculum, and its webbed toes also distinguish it from the last two. It is probably more closely related to P. neomexicanus than the other Western Plethodons. P. productus has a rather limited distribution. It is known only from Trinity, Humboldt, and Del Norte Counties, California; and Curry County, Oregon.

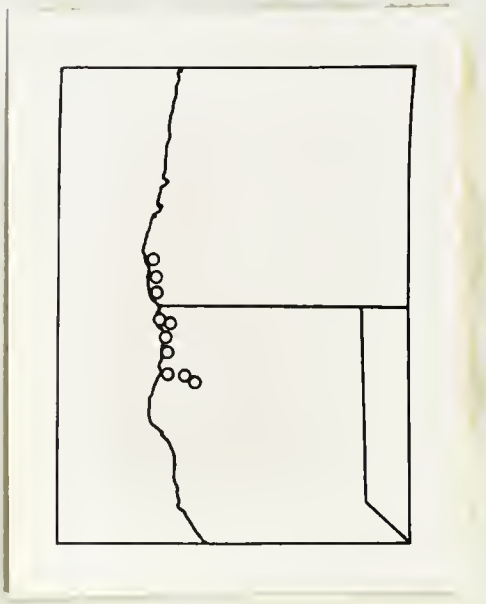

Figure 7. The distribution of Plethodon productus in California and Oregon.

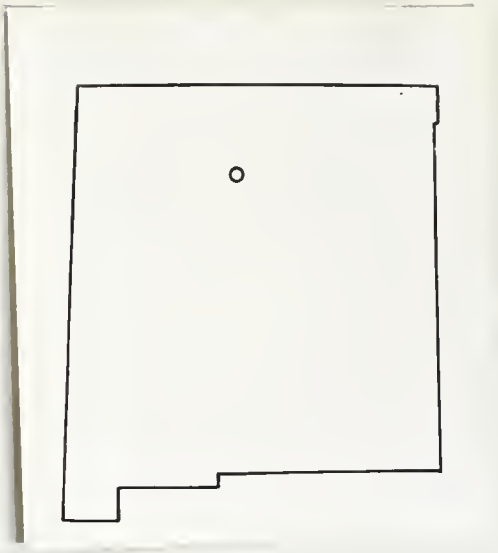

Figure 8. The distribution of Plethodon neomexicanus in New Mexico.

Stebbins (1951: 76) believes that specimens from the interior of the range differ in several respects from those on the coast.

Van Denburgh described this species in 1916, apparently without realizing that the name he proposed, elongatus, was a junior homonym of Salamandra elongata Valenciennes (in Dumeril and Bibron, 1854: 84) (= Plethodon glutinosus). This is a primary homonym due to the fact that the name elongata is available for Plethodon glutinosus, although the combination Plethodon elongatus has never been used for the slimy salamander. No subsequent worker has proposed a new name to replace the preoccupied name of the Del Norte salamander and it has always been referred to as Plethodon elongatus. This species has been known by the name elongatus since 1916 and it is unfortunate that the name has to be changed, but there is no alternative than to propose a new name in place of the preoccupied elongatus. The name productus also refers to the elongated condition of this species.

Plethodon neomexicanus Group

Plethodon neomexicanus Stebbins and Riemer

Eurycea multiplicata (Cope). Dunn (1926: 312-4, part).
Plethodon neomexicanus Stebbins and Riemer (1950: 73-80). Stebbins (1951: 76-9). Stebbins (1954: 58).

Type:- MVZ 49033, an adult male, collected 12 miles west and 4 miles south of Los Alamos, Sandoval County, New Mexico, at an altitude of about 8750 feet, by Robert Stebbins, on August 14, 1949.

Diagnosis:- A Western Plethodon with 20 trunk vertebrae.

Range:- Known only from the vicinity of the type locality in the Jemez Mountains of New Mexico, (figure 8).

Description:- This species has not been examined in life and reference should be made to the original description for an account of the pigmentation.

Costal grooves are usually 19, trunk vertebrae 20. Vomerine teeth range from 4 to 11 in a series in the 7 specimens examined. This is a large species, the type is over 70 mm. in snout-vent length. According to the data listed in Stebbins and Riemer (1950: 75), sexual maturity is not reached until approximately 50 mm. in snout-vent length.

This is an elongated salamander, with the largest number of trunk vertebrae of any of the western forms. It is unusual in that most specimens have only one phalanx on the fifth toe of the hind limb instead of the usual two phalanges. This is probably an intermediate stage in the loss of the fifth toe and reduction to the four-toed condition known to have occurred in several unrelated salamander genera.

The dorsal stripe is apparently absent in adults, but present in juveniles. This form is unique among the Western Plethodons in lacking the striped phase in the adult, and also in possessing a large number of brassy guanophores on the dorsum.

The Eastern Small Plethodons

The Eastern Small Plethodons are characterized by their small size. Except for P. welleri, they possess a higher number of trunk vertebrae and are relatively more elongate than the Eastern Large

Plethodons. Four species are included in this group. P. welleri has a restricted range, and is known only from a few counties in northwestern North Carolina and adjacent Tennessee and Virginia. P. richmondi is a polytypic form with three described races, and probably others which have not yet been defined. Its range centers in the Appalachian Plateaus Physiographic Province and it also occurs in immediately adjoining areas of several adjoining Provinces. P. cinereus, with three subspecies, has the widest range of any Eastern Small Plethodon, occurring over most of eastern United States and southeastern Canada, except in the region occupied by P. dorsalis. The range of P. dorsalis is centered in the Interior Low Plateaus Physiographic Province. P. d. angusticlavius is here regarded as a subspecies of dorsalis, rather than of cinereus, as originally described by Grobman (1944: 302).

The four species form a natural group of closely related forms. All possess webbed toes, a pigmented peritoneum, low vomerine tooth counts, brassy flecks on the dorsum, and white guanophore spots on the belly and sides. Two species, cinereus and dorsalis, are more similar to each other than either is to welleri or richmondi. Both cinereus and dorsalis typically possess at least as much white as black pigment on their bellies, and both are characterized by the presence of a red-backed phase in which there is a dorsal band of red or yellow lipophore pigmentation on the dorsum of the body and tail. In richmondi and welleri, the white pigment on the belly is limited to small spots and there is a much greater amount of black pigment than white. The red-backed phase, present in all of the races of dorsalis and cinereus,

is always absent in richmondi and welleri.

P. r. richmondi is the largest form, and also possesses the greatest number of trunk vertebrae, but both size and number of vertebrae are slightly reduced in the race popei, and decrease still more in the subspecies nettingi. Geographic variation in the number of trunk vertebrae is most pronounced in this species, with a range of 18 to 24 in all of the subspecies. P. welleri is less elongate and has fewer vertebrae than other small eastern species. It is unusual in its possession of ovarian eggs pigmented with melanophores, as well as in having an extremely dark parietal peritoneum. The brassy flecks on the dorsum of welleri are concentrated to form large patches, giving it a unique appearance not found in any other Plethodon. Its nearest relative is probably P. r. nettingi, but welleri is closest geographically to P. r. popei.

In most of their ranges, cinereus and dorsalis are allopatric forms, but in several areas where their ranges meet, there are records of the two occurring together in the same locality (see below). In each of these instances, there is no good evidence for hybridization or intergradation between the two forms, and for this reason they are usually considered as distinct species. They differ in several pigmentation characters, as well as in the average number of trunk vertebrae and the shape of the mental gland in adult males. P. dorsalis usually has 19 trunk vertebrae (range 18-20). Two races of cinereus typically have 20 trunk vertebrae (occasionally 19 or 21), while the third subspecies (polycentratus) usually has 21 or 22 (rarely 23) trunk vertebrae. In all of the Eastern Small Plethodons except dorsalis,

the mental gland is rather poorly developed and difficult to differentiate (except, perhaps, during the breeding season) from the adjacent portion of the chin. In dorsalis, on the other hand, it is a distinct rounded elevated gland, as in the Eastern Large Plethodons. Dunn (1926: 24) suggests that the striped pattern or dorsalis is more primitive than that of cinereus, since the paired red dorsal spots of several primitive plethodontids might be expected to pass through a zig-zag striped phase similar to that of dorsalis before evolving into a uniformly straight-edged stripe.

In 1944, Grobman described the narrow-striped populations occurring in southwestern Missouri and northwestern Arkansas as a distinct subspecies, Plethodon cinereus angusticlavius. This form possesses several characteristics that appear to link it more closely with dorsalis than with cinereus. It usually has 19 trunk vertebrae, as in dorsalis, while cinereus populations to the northeast and south of the range of angusticlavius usually have 20 trunk vertebrae. The mental gland is of the dorsalis type and in some specimens the dorsal stripe has irregular edges anteriorly, resembling very closely the pattern in dorsalis. Living specimens of angusticlavius have not been examined, so no accurate information is available on pigmentation characters, but the other characters strongly suggest that angusticlavius should be linked subspecifically with dorsalis rather than cinereus.

The elongation and increased number of trunk vertebrae in P. r. richmondi, P. r. popei, and P. c. polycentratus would appear to be a marked specialization of the usual plethodontid type. The forms welleri and dorsalis would appear to have retained more primitive char-

acteristics, but both have probably changed considerably from their common ancestor. The relationships of the Eastern Small Plethodons would appear to be best indicated by the phylogeny outlined in figure 9.

Plethodon welleri Group

Plethodon welleri Walker

Plethodon welleri Walker (1931: 48-51). Walker (1934: 190). Bishop (1943: 285-7). Grobman (1944: 313). Snyder (1946: 174). Hoffman and Kleinpeter (1948a: 107). Hoffman (1953: 86-7).

Type:- USNM 84135, an adult male, collected on Grandfather Mountain, at an altitude above 5000 feet, near Linville, North Carolina, by W. H. Weller and Ralph Dury, on August 27, 1930.

Diagnosis:- A dark-bellied, Eastern Small Plethodon with 17 trunk vertebrae and abundant dorsal brassy spotting.

Range:- From Yancey County, North Carolina, northeast in Tennessee and North Carolina to Mt. Rogers and White Top Mountain, Virginia (figure 10).

Description:- The dorsal pattern consists of large anastomosing patches of brassy guanophore spots. These spots appear to consist almost entirely of brassy guanophores, the white type of guanophore pigmentation present on the sides of welleri and on the dorsum of most plethodons, is not evident on the back of welleri. The brassy pigment is more concentrated than in any other form and the appearance of the dorsal spots is similar to the large white spots of glutinosus, except for the color,

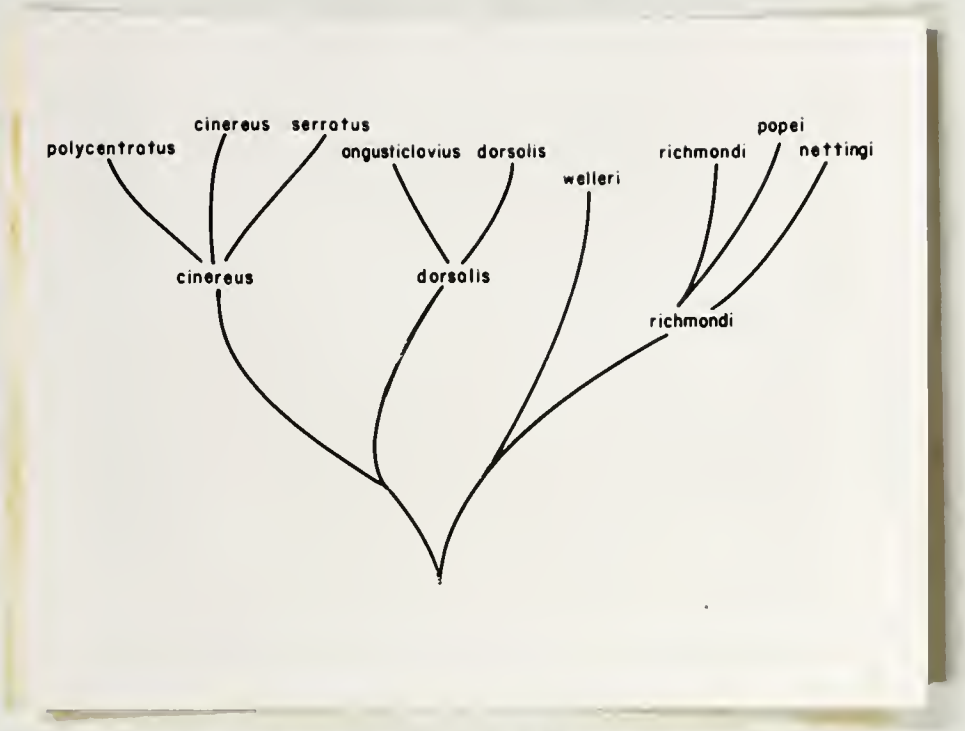

Figure 9. Suggested phylogeny of the Eastern Small Plethodons.

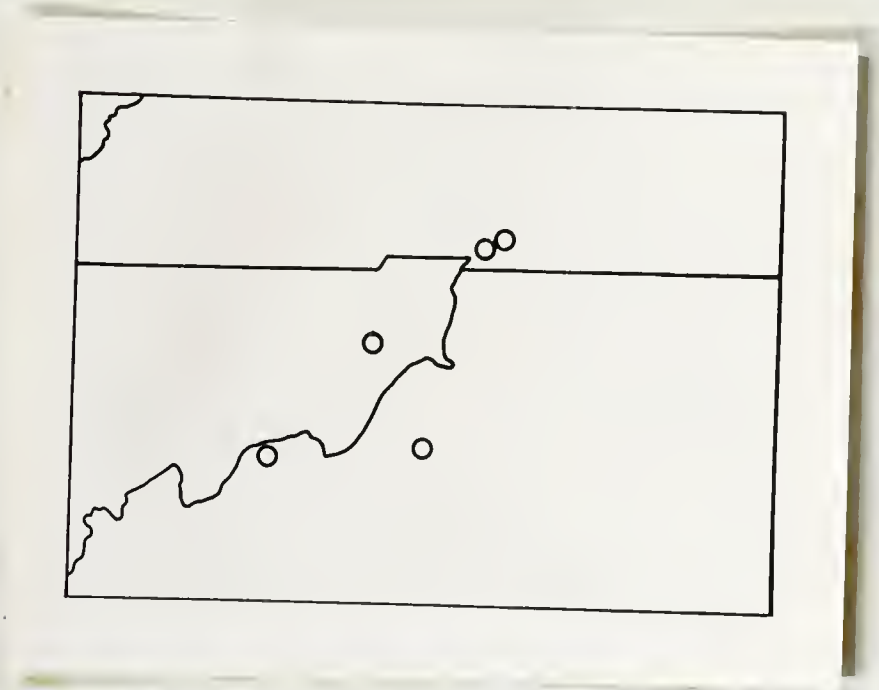

Figure 10. The distribution of Plethodon welleri in North Carolina, Tennessee, and Virginia.

which is brassy. Small white spots (0.1-0.2 mm.) are scattered over the belly and are similar to those of P. r. popei. The lateral spots (up to 1 mm. in diameter) are white with a slight amount of brassy flecking.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 2 to 7 in a series. In the 39 specimens examined, maximum known snout-vent length is between 45 and 50 mm. Sexual maturity is reached at about 35 mm. in snout-vent length.

P. welleri is the least elongate of all of the Eastern Small Plethodons, with the same number of trunk vertebrae (17) as in most of the Eastern Large Plethodons. In body build it resembles the large forms more than any other Eastern Small Plethodon. Its small size, vertebral structure, webbed toes, and pigmentation characters would appear to associate it more closely with the other small eastern forms.

This species has long been believed to be restricted to high elevations and was recorded only from Flat Top Mountain and Grandfather Mountain, North Carolina; and Mt. Rogers and White Top Mountain, Virginia. Recently, Hoffman (1953: 86) collected the species at an elevation of 2500 feet in Johnson County, Tennessee. I visited this locality during the summer of 1955, and although conditions were very dry, succeeded in collecting one young specimen, thus confirming Hoffman's record. This species may well occur in suitable habitats at low altitudes throughout the region.

Walker (1934: 190) has pointed out that individuals from White Top Mountain, Virginia, possess more spots on their venters than individuals from the type locality, Grandfather Mountain, North Carolina.

Specimens from Mt. Rogers (USNM 124421-9) also possess spotted bellies. One specimen from Flat Top Mountain, Yancey County, reported by Snyder (1946: 174) is also described as having a more conspicuous mottling on the venter. Perhaps the Grandfather Mountain population is unusual in lacking this characteristic. The low altitude specimen from Tennessee has a greater amount of dorsal brassy pigment than eight living topotypes from Grandfather Mountain. I have not examined living specimens from any of the other localities.

P. welleri is unusual in possessing dark ovarian eggs that are pigmented with melanophores. Its closest relative is probably P. richmondi, which it resembles by the presence of a dark belly. P. r. nettingi usually has 19 trunk vertebrae, although occasional specimens possess 18 or 20. Since a small percentage of welleri also have 18 trunk vertebrae (table II), there is slight morphological overlap between the two forms in this character.

TABLE II

THE NUMBER OF TRUNK VERTEBRAE IN GEOGRAPHIC SAMPLES OF PLETHODON WELLERI

Locality	Number of trunk vertebrae		
	16	17	18
Grandfather Mountain, North Carolina		25	
Johnson County, Tennessee		1	
White Top Mountain, Virginia		4	
Mt. Rogers, Virginia	1	6	2

Plethodon richmondi

In 1938, two new Eastern Small Plethodons, P. richmondi and P. nettingi, were described by Netting and Mittleman (1938: 297) and Green (1938: 295). Both are characterized by their dark bellies and brassy dorsal flecking. Available samples of richmondi from Ohio and West Virginia possess 20 to 22 costal grooves (21 to 23 trunk vertebrae), while P. nettingi has 17 to 19 costal grooves (18 to 20 trunk vertebrae). They both differ from P. c. cinereus in the number of vertebrae, and they are distinguished from the entire cinereus group by their dark bellies and lack of red pigment. Most previous writers are in agreement that these two forms, richmondi and nettingi, are more closely related to each other, and to welleri, than they are to cinereus and dorsalis (Netting and Mittleman, 1938: 292; Green: 1938: 298; Grobman, 1944: 311).

In 1949, Grobman described another flecked plethodon (P. huldae) which he assigned to this group because of its heavily flecked dorsum. This form possesses 20 trunk vertebrae, the same as cinereus, and also has a mottled belly as in cinereus. Rabb (1955: 261-3) and Muchmore (1955: 170-2) present convincing evidence that huldae, although possessing brassy dorsal flecks similar to those of richmondi and nettingi, is actually based on dark-phase specimens of P. cinereus. Muchmore (1955: 172) goes so far as to state that "since P. c. cinereus possesses brassy flecks on the dorsum and since P. huldae can no longer be considered valid, it is certainly desirable that the concept of a welleri group of Plethodon distinct from a cinereus group be abandoned." Obviously these forms are all more closely related than any of them are to the Eastern Large Plethodons or the Western Plethodons, yet the fail-

ure of one suggested character to define the group should have no bearing on the fact that other features are useful in distinguishing it (dark belly and lack of red dorsal stripe).

Netting and Mittleman (1938: 292) state that specimens of P. richmondi from Watauga County, North Carolina, differ from typical richmondi, but do not give any evidence to support this contention. Neither Bishop (1943: 239) nor Grobman (1944: 312) include this locality in their distribution maps of the range of richmondi, although Grobman mentions the literature reference to the North Carolina specimens. More recently, Hoffman and Hubricht (1954: 192) report richmondi from several localities in southwestern Virginia and northwestern North Carolina, but do not find any consistant differences between these specimens and topotypes of richmondi. A study of their material and large series from this area in the University of Florida Collection have shown, however, that these southern richmondi are actually quite distinct in the number of trunk vertebrae from more northern richmondi. This southern form has recently been described as a new subspecies of richmondi, P. r. popei, by Highton and Grobman (in press). No other character could be found to distinguish preserved specimens of popei and richmondi. Living specimens of P. r. richmondi have not been available during this study, so it has not been possible to compare the pigmentation characters of the two forms.

On the basis of the slight overlap in distinguishing characters, as well as the geographic replacement of the three forms, richmondi, popei, and nettingi, Highton and Grobman (in press) suggested that they should all be considered subspecifically related. One

matter, not discussed in their paper, is the apparent sympatric relationship of nettingi and richmondi. Although the two forms, to my knowledge, have not been collected at the same locality, the entire range of nettingi, as summarized by Brooks (1948), is surrounded by records of richmondi.

Thurow (1955) has recently reported nettingi from Bedford County, Virginia, a locality about equidistant from the nearest known nettingi and popei localities. An examination of these specimens (CNHM 60512-8) confirms Thurow's suggestion that they belong to this group. Although they are poorly preserved, their dark bellies indicate that they are not dark-phase cinereus. They differ from both nettingi and popei, however, in costal groove count. Five of the seven specimens have 19 costal grooves, while the other two have 18. The sample is small, but the probability that they were taken from a population of nettingi similar to that in Randolph and Pocahontas Counties, West Virginia, which has 19 costal grooves less than 5% of the time, is very low. Four of the seven Bedford County, Virginia, specimens have 20 trunk vertebrae, two possess 19, and the remaining specimen is too small to obtain an accurate count from the radiograph, but it probably also has 20 trunk vertebrae, since it has 19 costal grooves. The population from which these specimens were collected probably represents an intermediate one between popei and nettingi. If the usual number of trunk vertebrae is 20, and this occurs with high frequency, this population should probably be given separate subspecific nomenclatorial status. At present, with only seven poorly preserved specimens available, too little is known of its variation to described it as new here. Its importance lies in the fact that an intermediate population, often

possessing 20 trunk vertebrae, is known from a locality between the ranges of nettingi (usually with 19 trunk vertebrae) and popei (usually with 21 trunk vertebrae). This may be considered further evidence that nettingi and popei are subspecifically related.

In the Valley and Ridge Province of Virginia, there exists a population of P. r. richmondi which Hoffman and Hubricht (1954: 192) believe to be different in both color and structural features from other populations of P. richmondi. They do not state the ways in which it differs, but an examination of preserved specimens from this region (Alleghany and Rockingham Counties, Virginia) indicates that these animals, although possessing a vertebral count similar to richmondi, differ from it in having a mottled belly. Specimens from these counties are easily segregated from topotypical richmondi and popei on the basis of the character of the belly. In ten specimens of the mottled bellied form for which vertebral counts are available, six possess 22, three 23, and one 24 trunk vertebrae. The average is slightly higher than the usual richmondi number, but does not differ significantly from it. It is quite likely that examination of living specimens, and the accumulation of more data on vertebral counts may reveal differences which will indicate that this population represents a distinct nominal form. Specimens from other areas in the Valley and Ridge Province should be studied in order to delimit the range of the mottled-bellied richmondi.

The distribution of these forms indicates that there is probably a series of five races, two of them undescribed, each of which replaces its nearest relative geographically. One extreme (nettingi) occurs sympatrically with the two at the other extreme (richmondi and

the undescribed Virginia Valley and Ridge animal). Table III shows the variation in the vertebral counts of these populations.

TABLE III

GEOGRAPHIC VARIATION IN THE NUMBER OF TRUNK VERTEBRAE IN PLETHODON RICHMONDI

Sample	Number of trunk vertebrae							
	18	19	20	21	22	23	24	Mean
P. r. nettingi	1	22	1					19.0
Bedford County, Virginia		2	4					19.7
P. r. popei			4	51	12			21.1
P. r. richmondi				4	30	9		22.1
Alleghany and Rockingham Counties, Virginia					6	3	1	22.5

The races of richmondi appear to form a ring of subspecies, none of which is completely distinct morphologically from the related adjacent form (or forms). P. r. nettingi is not known below 3550 feet elevation in the Cheat Mountains of West Virginia (Brooks, 1948) and it thus may be completely isolated ecologically from P. r. richmondi. There is no information on the upper altitudinal limits of richmondi in the literature, but it is known from localities throughout most of West Virginia. A similar case has been reported by Stebbins (1949) for the western salamander genus Ensatina, in which the two end forms of an allopatric series of subspecies occur in immediately adjacent regions

without any evidence of interbreeding. An accurate knowledge of the ecological distribution of the overlapping forms of P. richmondi is lacking. There appears to be little or no overlap between the two terminal races of Ensatina eschscholtzi, whereas in this case, one (nettingi) definitely occurs within the range of richmondi, for there are records of the latter to the north of the Cheat Mountains in Pennsylvania, to the east and west in West Virginia, and to the south in Virginia.

In these series of populations we probably see the stages through which the subspecies of richmondi have differentiated. All of the forms probably have changed somewhat from the original stock, but the close similarity of all the forms, except for the number of body segments, would seem to indicate that this change has not been great. It is difficult to determine which form most closely resembles the ancestral condition. P. r. richmondi is unlike most plethodons in its elongate form and would appear highly specialized. On the other hand, it wide distribution and the fact that the eastern Valley and Ridge population has a mottled belly, approaching that of the cinereus group, might be considered evidence that this form is a more primitive generalized animal. It is possible to reconcile these viewpoints, for it is often found that a given form is specialized in some ways, yet retains certain other primitive characteristics.

Since P. r. nettingi is apparently limited to high altitudes in the Cheat Mountains, it could be interpreted either as a specialized type adapted to this habitat, or as a relict of a once more widely distributed spruce forest population. At present, the evidence is not sufficient to choose between the two alternatives. On the basis of its

fewer trunk vertebrae, nettingi would appear to be less specialized than the other subspecies.

Intergradation between the races of richmondi may occur in certain regions. P. r. nettingi may now be completely isolated from its nearest relative, but the ranges of popei and richmondi probably meet in eastern Kentucky, and intergradation might be expected. Large samples from critical areas will be necessary before conclusive evidence is obtained, since intergrades between popei and richmondi, for example, would be expected to possess about an equal number of specimens with 21 and 22 trunk vertebrae. Large series of specimens from each county in and on both sides of the area of intergradation would be necessary to determine its extent. Such series are not now available from Kentucky, and hollow symbols representing literature records for this region on the distribution map (figure 11), may represent popei, intergradient, or richmondi populations.

Plethodon richmondi richmondi Netting and Mittleman

Plethodon richmondi Notting and Mittleman (1938: 287). Netting (1939: 50-1). Dury and Gessing (1940: 31). Bishop (1943: 272-5). Grobman (1944: 312). Wood (1945a: 49). Wood (1945b: 206-10). Netting (1946: 12). Wood (1946: 169). Wood and Duellman (1947: 3). Grobman (1949: 135). Richmond (1952: 314). Green and Walker (1954: 60). Duellman (1954: 40-5). Hoffman and Hubricht (1954: 191-3). Plethodon richmondi richmondi Netting and Mittleman. Highton and Grobman (in press).

Type:- CM 14189, an adult male, collected in Ritter Park, Huntington,

Cabell County, West Virginia, at an elevation of 600-700 feet, by Neil D. Richmond and N. Bayard Green, on October 15, 1938.

Diagnosis:- A dark-bellied Eastern Small Plethodon, usually with 22 trunk vertebrae (range 21-24), which completely lacks red pigment.

Range:- From Centre County, Pennsylvania, south through western Maryland, West Virginia, and northwestern Virginia, west to northeastern Kentucky, and north to southern and eastern Ohio (figure 11).

Description:- This form has not been examined in life and nothing on the pigmentation can be added to previously published accounts.

The costal grooves usually number 21, the trunk vertebrae 22. Vomerine teeth range from 3 to 9 in a series. This is the largest Eastern Small Plethodon, the largest specimen examined, from Alleghany County, Virginia, is 60 mm. in snout-vent length.

Plethodon richmondi popei Highton and Grobman

Plethodon richmondi Netting and Mittleman. Barbour (1953: 85-6).
Hoffman and Hubricht (1954: 191-3).
Plethodon richmondi popei Highton and Grobman (in press).

Type:- UF 8226, a maturing male, collected at Comers Rock, Grayson-Wythe County line, Virginia, by Arnold B. Grobman and Marc R. Grobman, on August 5, 1955.

Diagnosis:- A race of Plethodon richmondi that usually possesses 21 trunk vertebrae (range 20-22).

Range:- Known from Harlan County, Kentucky; Tazewell, Smyth, Grayson,

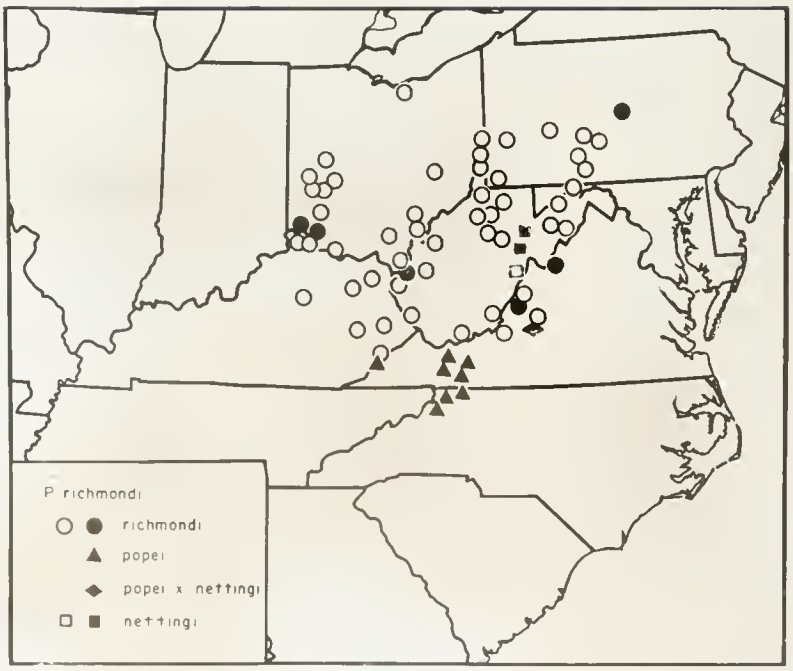

Figure 11. The distribution of the subspecies of Plethodon richmondi. Solid symbols represent localities from which specimens have been examined. Hollow symbols, represent literature records.

and Wythe Counties, Virginia; and Ashe, Alleghany, and Watauga Counties, North Carolina (figure 11). This form may have a greater range than now known. Specimens from adjacent Kentucky and West Virginia have not been examined. They may also belong to this race.

Description:- Living specimens possess both types of guanophore spots on the dorsum. Small brassy flecks are very abundant and larger white spots are also present. On the sides and venter there are larger white or yellow spots.

The costal grooves usually number 20, the trunk vertebrae 21. Vomerine teeth range from 3 to 8 in a series. The largest specimen examined is 48 mm. in snout-vent length. Sexual maturity is reached between 35 and 45 mm. in snout-vent length.

Plethodon richmondi nettingi Green

Plethodon nettingi Green (1938: 295-9). Bishop (1943: 266-9). Grobman (1944: 313). Brooks (1945: 231). Brooks (1948: 239-44).
Plethodon richmondi nettingi Green. Highton and Grobman (in press).

Type:- CM 10279, an adult male, collected on Barton Knob, near Cheat Bridge, Randolph County, West Virginia, at an elevation of about 4000 feet, by M. Graham Netting, on June 29, 1935.

Diagnosis:- A race of Plethodon richmondi that usually possesses 19 trunk vertebrae (range 18-20).

Range:- Known from altitudes above 3500 feet in the Cheat Mountains of Randolph and Pocahontas Counties, West Virginia (figure 11).

Description:- In life, the dorsum of this form is similar in coloration to P. r. popei. The costal grooves usually number 18, the trunk vertebrae 19. Vomerine teeth range from 3 to 8 in a series. The largest specimen examined is 45 mm. in snout-vent length. This form appears to have a smaller average size than the other races of richmondi. Sexual maturity is reached at about 35 mm. in snout-vent length.

Plethodon cinereus Group

Plethodon dorsalis

The range of P. dorsalis centers in the Interior Low Plateaus Physiographic Province, but does not appear to be restricted to it, for records are available from several adjacent provinces. This species has not heretofore been recorded from Georgia, but specimens are now available from four different localities in that state, three of which are in the Piedmont Province. The southernmost record is from Upson County (UMMZ 85574), only a few miles above the Fall Line. Other records are for Henry County (UF 8371 (3), UF 8413 (3)); Cobb County (UG 206 (6); UG 275 (36)); and Dade County (ERA-WTN 12128 (12)). Probably the natural range of this form includes the western part of the state above the Fall Line.

The sympatric occurrence of this species with P. cinereus in Georgia, Tennessee, Indiana, Illinois, and Oklahoma will be discussed below. The two forms are very similar in appearance, and it is often difficult to identify individual specimens. For this reason a detailed study of the two species in the areas of overlap will be necessary be-

fore it can be determined whether or not hybridization occurs.

In Georgia, where there is no overlap in the vertebral counts of the two species, it is impossible, on other grounds, to identify a small percentage of the available specimens. There are, however, several differences between the two species in Georgia that are apparent in a large majority of the available specimens. These include the shape of the mental gland in adult males; the zig-zag stripe of dorsalis, compared to the straight-edged stripe in cinereus; the presence of more red pigment in front of the eyes on the head of dorsalis; the great reduction in amount of melanophore pigmentation on the belly of dorsalis; and a similar reduction in red lipophore pigmentation on the belly of cinereus. The fact that there are a few exceptions to each of these species characteristics might be considered evidence for hybridization were it not for the fact that occasional specimens of each species from localities in which the other form is absent show at least some of the same variations from the usual pattern. The fact that there is no tendency toward an increase in the number of trunk vertebrae in Georgia dorsalis populations is also significant (see table IV). It may be seen from this table that there is no strong tendency for an increase in the number of vertebrae in samples of dorsalis that are from areas in which geographic overlap with cinereus occurs. We may conclude that there is, as yet, no good evidence for hybridization between the two species, but that more study is needed in all of the areas in which the two occur together.

There are no available records of dorsalis in southeastern Missouri. This region should be explored in order to determine whether or not dorsalis or angusticlavius are present. Smith (1948: 1) has

recently reported dorsalis from several localities in southeastern Illinois.

TABLE IV

THE NUMBER OF TRUNK VERTEBRAE IN SAMPLES OF PLETHODON DORSALIS

Sample	Number of trunk vertebrae		
	18	19	20
P. d. dorsalis			
Georgia*	2	49	2
Alabama		2	
Tennessee			
Great Smoky Mountains*		34	9
Van Buren County	1	44	6
Marion County		2	
Indiana*		1	2
P. d. angusticlavius			
Arkansas		23	5

* Areas in which cinereus and dorsalis have been taken together at the same locality.

Dunn (1926: 162) states that the unstriped phase in dorsalis is confined to adults and that this phase is much lighter than the dark phase of cinereus. The latter part of his statement appears to be true, but in a series of 31 living specimens of dorsalis from Van Buren County, Tennessee (UF 8394), there are five juveniles (16 to 18 mm. snout-vent length) that are definitely of the dark phase. As in adults, there is

a slight amount of red pigment in the region of the back in which the stripe is located in red-backed individuals, so that an outline of the irregular stripe can be seen when held at a certain angle to the light. The presence of the red pigment, as well as a reduction in the melanophore pigmentation does give the lead-backed phase of dorsalis a lighter appearance than the corresponding phase of cinereus.

Grobman (1944: 308) presents evidence to show that Baird should be credited with the authorship of the name dorsalis. Under Article 21 of the International Rules of Zoological Nomenclature as of 1944, he was correct. Since 1944, however, the Rules have been amended, so that Cope should now be recognized as responsible for this name.

Plethodon dorsalis dorsalis Cope

Plethodon cinereus dorsalis Cope (1889: 138-9). Blanchard (1926: 368-9). Bishop (1943: 236-9). Parker (1948: 22). Chermock (1952: 29).

Plethodon erythronotus (Green). Garman (1894: 38).

Plethodon dorsalis Cope. Stejneger and Barbour (1917: 15). Dunn (1918: 460-2). Dunn (1926: 158-62). Mohr (1937: 40). Parker (1937: 63). Parker (1939: 75). King (1939: 550-1). Swanson (1939: 687). Grobman (1944: 308-11). Smith (1948: 1). Sinclair (1950: 50). Mohr (1952: 59-60). Thurow (1955: 62-3). Holman (1955: 143).

Type:- USNM 3776, collected at Louisville, Jefferson County, Kentucky.

Diagnosis:- An Eastern Small Plethodon with the usual number of trunk vertebrae 19 (range 18-20), and a red dorsal stripe with irregular edges

in the red-backed phase.

Range:- From southern Illinois, Indiana, and southeastern Ohio, south through Kentucky and Tennessee to northern Alabama and northwestern Georgia (figure 12).

Description:- The dorsum of both color phases of P. d. dorsalis has small white spots (0.2-0.4 mm.) as well as smaller brassy flecks. The red-backed phase, in addition to the other pigments, contains a large amount of red lipophore pigment. All of these chromatophores appear to be identical with those of P. cinereus. The main difference between the two species is in the abundance and distribution of the pigments. The melanophore background in dorsalis is somewhat reduced, giving the animal an overall lighter appearance than cinereus. The melanophore pigment on the belly of dorsalis is greatly reduced with a corresponding increase in the amount of red lipophores, so that the belly appears to be mottled with red and white rather than black and white, as in cinereus. In dorsalis there is a concentration of red pigment on the head in front of the eyes. The lateral guanophore pigment is often yellowish in color. The dorsal red stripe is quite variable. In some specimens the edges are irregular for the entire length of the body, while in others, they are irregular only in the anterior half or third of the body. The latter condition is especially common in Georgia specimens, and occasional specimens from Georgia have straight-edged dorsal stripes as in cinereus. Specimens with straight-edged dorsal stripes have been reported also from Indiana (Blanchard, 1926: 369) and Tennessee (Grobman, 1944: 309-10).

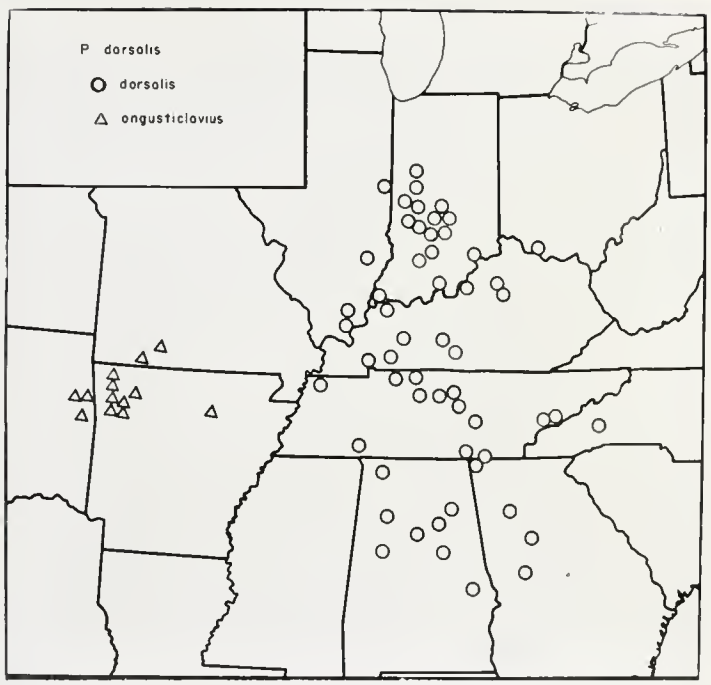

Figure 12. The distribution of the subspecies of Plethodon dorsalis.

The costal grooves usually number 18, the trunk vertebrae 19. Vomerine teeth range from 3 to 6 in a series. This is a small species; sexual maturity is probably reached at about 30 mm. in snout-vent length. The largest specimen examined is 44 mm. in snout-vent length.

Plethodon dorsalis angusticlavius Grobman

Plethodon cinereus angusticlavius Grobman (1944: 302). Dundee (1947: 117). Bragg and Hudson (1951: 89). Bragg (1955: 27-8).

Type:- AMNH 40366, an adult male, collected at Mud Cave, near Fairy Cave, Stone County, Missouri, by B. C. Marshall, on October 1, 1927.

Diagnosis:- A race of Plethodon dorsalis in which the width of the dorsal band is usually less than one-third of the width of the body.

Range:- Southwestern Missouri, northwestern Arkansas, and adjacent Oklahoma, north of the Arkansas River (figure 12).

Description:- Living specimens of this form have not been examined. Of 33 preserved specimens (all from Arkansas), 10 are of the striped phase, 11 show no trace of a stripe, and the remainder show only a faint stripe on the body, but at the base of the tail, it widens and becomes much more well-defined. Typically striped angusticlavius also possess a wider and brighter dorsal stripe at the base of the tail than on the body. The brightness of the stripe in this region appears to be due to a reduction in melanophore pigmentation in the dorsal stripe. The dorsal stripe is often irregular anteriorly, as in dorsalis.

The costal grooves usually number 18, the trunk vertebrae 19. Vomerine teeth range from 4 to 8 in a series. The largest specimen

examined is 43 mm. in snout-vent length.

Plethodon cinereus

The red-backed salamander is the most abundant terrestrial salamandor over most of its range, which includes much of eastern North America. Two distinct color phases are present, one with a prominent red or yellow dorsal stripe, the other uniformly dark in appearance. The frequency of these color phases varies from one locality to another. In some places, both phases occur in approximately equal numbers, in others, one type may be rare or absent. The proportional distribution of these color phases in the various populations has recently been studied by Thurow, and it is hoped that the results of his work will be published in the near future. Occasional specimens have been reported that lack the dark pigment and appear entirely red. One specimen from New Jersey lacked the red pigment in life and had a colorless dorsal stripe.

Plethodon dorsalis has been considered a subspecies of P. cinereus by some workers (Cope, 1889: 138; Blanchard, 1926: 269; Bishop, 1943: 236), and as a distinct species by others (Dunn, 1926: 158; Grobman, 1944: 308). Grobman points out that although the two forms are largely allopatric, at some localities, especially in southern Indiana, the two occur together, Grobman examined the series of dorsalis that King (1939: 551) reported from the Great Smoky Mountains of Tennessee and confirmed their identification. Specimens of both species found together at the same localities are represented in the GSMNP collection. These localities are White Oak Sinks (elevation 1750 feet) and the Sinks

on the Little River (elevation 1600 feet). On the Tennessee side of the Great Smoky Mountains, P. cinereus is known from 1600 to 5000 feet and P. dorsalis from 1200 to 2200 feet.

The two species also occur sympatrically in the Piedmont of western Georgia. At two localities, 3.8 miles north of McDonough, Henry County; and 8.5 miles north of Thomaston, Upson County, the two species have been taken together. At all other localities in western Georgia, where either P. c. polycentratus or P. d. dorsalis have been collected, the other form has not been taken.

Bragg (1955:.27) reports that he collected a specimen of P. c. serratus and a specimen of P. d. angusticlavis at the same locality in Cherokee County, Oklahoma. Apparently the two species often occur together where their ranges overlap. Smith (1948: 1) published several new records of dorsalis from southeastern Illinois. P. cinereus and P. dorsalis probably also occur sympatrically in that state. There appears to be no evidence of intergradation at any of these localities, confirming the conclusion of Dunn and Grobman that dorsalis and cinereus have reached the species level of differentiation.

P. cinereus shows little apparent geographic variation over most of its range, except in the frequency of occurrence of the two color phases referred to earlier. Only in the Piedmont of Georgia and in Arkansas and Oklahoma, where the populations of this species have apparently become isolated from the parent stock, so we find differentiation of the magnitude required for the recognition of subspecies. The Arkansas and Oklahoma race (serratus) possesses a dorsal band with

serrations at each costal groove. This characteristic is sometimes slightly developed in some specimens of other populations, but never reaches the frequency of occurrence or degree of development present in serratus.

The Georgia Piedmont subspecies (polycentratus) differs from other populations of cinereus in its increased number of trunk vertebrae. Data on the number of trunk vertebrae in samples of P. cinereus are listed in table V. It also differs from most cinereus in possessing red pigment on the belly between the front limbs. The cinereus populations in western North Carolina and eastern Tennessee are characterized by the complete absence of the dark lead-backed phase. P. c. polycentratus differs from these adjacent cinereus populations by the presence of the lead-backed phase (38% of the type series of polycentratus are dark phase).

Sanders and Smith (1949: 28) report a specimen of Plethodon cinereus from Fern Lake, near Nacogdoches, Nacogdoches County, Texas. This specimen (OS 556) lacks the serrate edges in the dorsal stripe that are present in serratus, the nearest race geographically. It has 19 trunk vertebrae, but this number is not unusual in other populations of cinereus. Mr. Sanders, who collected the specimen, informs me (in letter of November 12, 1955) that it was taken with a dip net from a bunch of fruiting sphagnum moss near the shore line, a most unusual habitat for this terrestrial species. It may represent an accidental introduction by man, and the record needs confirmation by the collection of additional specimens from Texas before this state can be included in

the natural range of this species.

TABLE V

GEOGRAPHIC VARIATION IN THE NUMBER OF TRUNK VERTEBRAE OF PLETHODON CINEREUS

Locality	Number of trunk vertebrae				
	19	20	21	22	23
P. c. cinereus					
New Brunswick, Canada	3	14	1		
Nova Scotia, Canada	2	2	1		
Quebec, Canada	1	1			
Indiana		6	2		
Missouri		1			
New Jersey		7			
Virginia (Blue Ridge Province)	7	33	3		
Eastern Tennessee and western North Carolina	5	40	9		
P. c. serratus					
Arkansas	3	19			
P. c. polycentratus					
Georgia			21	24	2

Plethodon cinereus cinereus (Green)

Salamandra cinerea Green (1818: 356).

Salamandra erythronota Green (1818: 356). (Type locality, probably vicinity of Princeton, New Jersey.)

Plethodon cinereus (Green). Tschudi (1838: 58). Dunn (1926: 163-80).

Sauropsis erythronotus (Green). Fitzinger (1843: 33).

Plethodon erythronotus (Green). Baird (1850: 285).

Ambystoma erythronotum (Green). Gray (1850: 37).

Salamandra puncticulata Valenciennes in Dumeril and Bibron (1854: 87).

Salamandra agilis Sager (1858: 429). (Type locality, Detroit, Michigan)

Plethodon erythronotus cinereus (Green). Cope (1869: 99).

Plethodon cinereus cinereus (Green). Davis and Rice (1883: 26). Bishop (1941: 196-219). Bishop (1943: 232-6). Grobman (1944: 300-2).

Plethodon cinereus erythronotus (Green). Cope (1889: 135).

Plethodon huldae Grobman (1949: 136). (Type locality, Hawksbill Mountain, Madison County, Virginia.)

Type:- Dunn (1926: 165) states that the type is not known to exist. The type locality is probably in the vicinity of Princeton, New Jersey.

Diagnosis:- A Small Eastern Plethodon with a black and white mottled belly; usually with 20 trunk vertebrae; and a straight-bordered dorsal stripe in the red-backed phase.

Range:- Nova Scotia, New Brunswick, southern Quebec and Ontario, Canada; south through the eastern United States to North Carolina, eastern Tennessee and Kentucky, Ohio, Indiana, Illinois and southeastern Missouri (figure 13).

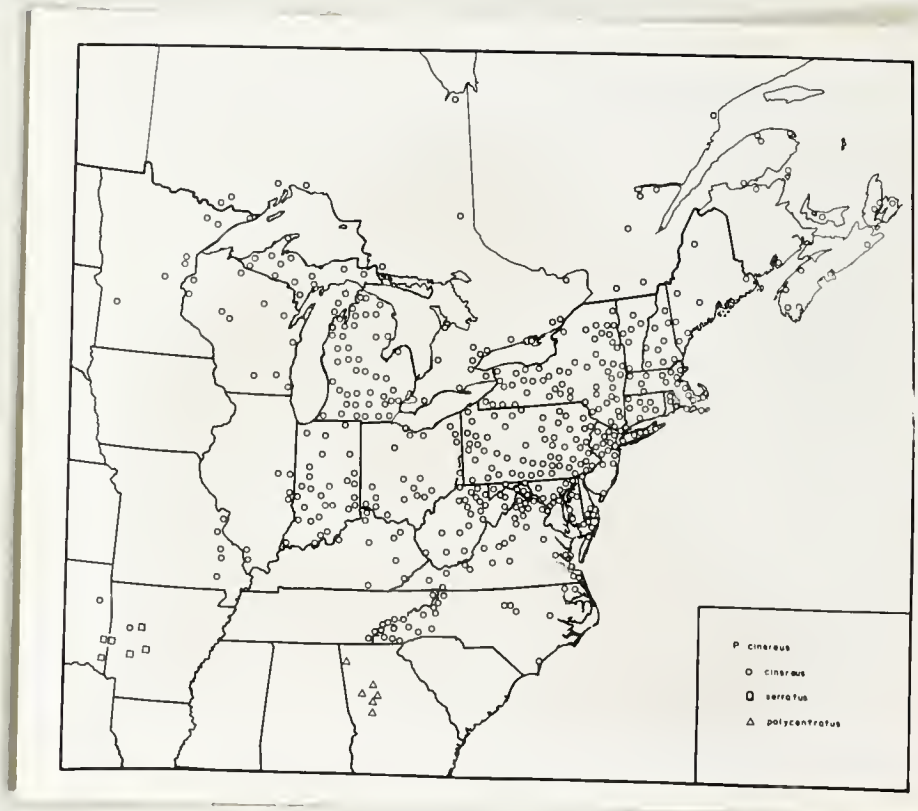

Figure 13. The distribution of the subspecies of Plethodon cinereus.

Description:- The dark, unstriped phase is usually characterized by the absence of red lipophores, the presence of small white spots on the dorsum (0.07-0.2 mm in diameter), and numerous smaller brassy flecks on the head, back, and tail. The belly is mottled with black and yellow or white guanophores. The lateral guanophore pigment is similar to that on the belly.

The red-backed phase has sides and belly similar to the dark phase. The white spots and brassy flecks on the dorsum are reduced in the area of the dorsal stripe, but are present on the head and tail. The color of the lipophores in the dorsal stripe is variable, ranging from red to yellow.

The costal grooves usually number 19, the trunk vertebrae 20. Vomerine teeth range from 3 to 9 in a series. The largest specimen examined is 51 mm. in snout-vent length. Sexual maturity is reached at about 35 mm. in snout-vent length.

Plethodon cinereus serratus Grobman

Plethodon cinereus serratus Grobman (1944: 306-8). Bragg (1952: 244). Bragg (1955: 27-8).

Type:- CNHM 39464, a female, collected on Rich Mountain, Polk County, Arkansas, at an elevation of 2500 feet, by Karl P. Schmidt and C. M. Barber, on March 23, 1938.

Diagnosis:- A race of Plethodon cinereus in which the edges of the dorsal stripe are serrated at each costal groove.

Range:- West-central uplands of Arkansas and adjacent Oklahoma, south of the Arkansas River (figure 13). Also reported by Bragg (1955: 27-8) from Cherokee County, Oklahoma (north of the Arkansas River).

Description:- The dark phase is apparently rare in this form, only one of 33 specimens examined lacked the red dorsal band. In red-backed individuals, the serrations on the edges of the dorsal stripe are present on the body, but not on the tail. The serrations are due to the fact that the red pigment in the dorsal stripe extends ventrolaterally toward the top of each costal furrow. The usual absence of melanophores in this extension of the dorsal stripe makes the saw-tooth edge of the stripe conspicuous to the naked eye.

The costal grooves usually number 19, the trunk vertebrae 20. Vomerine teeth range from 3 to 8 in a series. The largest specimen examined is 46 mm. in snout-vent length.

Plethodon cinereus polycentratus Highton and Grobman

Plethodon cinereus polycentratus Highton and Grobman (in press).

Type:- UF 8376, an adult male, collected 2 miles northeast of Palmetto, Fulton County, Georgia, by Albert H. Highton and Richard Highton, on February 2, 1954.

Diagnosis:- A race of Plethodon cinereus in which the usual number of trunk vertebrae is 21 or 22 (rarely 23).

Range:- The Piedmont of western Georgia (figure 13).

Description:- This race is similar in coloration to the typical sub-

species. It differs in possessing a greater number of body segments. Vomerine teeth range from 3 to 7 in a series. The largest specimen is 42 mm. in snout-vent length. Sexual maturity is reached at about 35 mm. in snout-vent length.

The Eastern Large Plethodons

This group, as defined by Grobman (1944: 266) on the basis of larger size and fewer costal grooves than the other eastern plethodons, includes six species that inhabit the eastern portion of the United States. Plethodon glutinosus is the most widely distributed and all the other species occur within its range. P. yonahlossee occurs in the Southern Section of the Blue Ridge Province north of the French Broad River. P. ouachitae, superficially very similar to yonahlossee, lives in the Ouachita Mountains of Arkansas and Oklahoma. The recently described P. caddoensis is known only from the Caddo Mountains of Arkansas. P. jordani includes eight subspecies, all occurring in the Southern Section of the Blue Ridge Province. The range of P. wehrlei is centered in the Unglaciated Allegheny Plateau Section of the of the Appalachian Plateaus Province. (See Grobman (1944) for an analysis of the distribution of these forms.) Two recently described species, P. dixi and P. jacksoni are here considered races of wehrlei, because of their close morphological similarity to wehrlei and the fact that they replace wehrlei geographically.

There has been much speculation on the relationships of the species within this section of the genus. Dunn (1926: 23) believes this to be the most primitive group of the genus, with yonahlossee the

most primitive form. Dunn and Grobman (1944: 276) both believe the relationship between yonahlossee and wehrlei is close. Hairston and Pope (1948) suggest that yonahlossee is closely related to jordani and that close similarity between some jordani and glutinosus is merely convergence, but others think that the closest relative of jordani is glutinosus. Bishop (1941) even considered one race of jordani (shermani) to be racially related to glutinosus. On the other hand, Grobman (1944) believed that jordani and closely related forms (now all considered races of jordani) are different enough to warrant the erection of a separate group, that he called the metcalfi group, distinct from all the other Eastern Large Plethodons.

Characters studied by previous workers in attempting to determine the morphological similarity and hence the relationships of these forms, include size, number of vomerine teeth, number of costal grooves, degree of sexual dimorphism, and pigmentation. In the present study, most of these characters have been reexamined using large series of specimens that, for the most part, were not available to previous workers. Several characters have been found to be extremely variable and not diagnostic of any one form. For example, Bishop (1941: 18), Grobman (1944: 287), and Hairston and Pope (1948: 274) all believed that the Plethodon jordani group has fewer vomerine teeth than P. glutinosus. I have counted the vomerine teeth of 269 Florida glutinosus (figure 14), 125 Virginia glutinosus (the same specimens used by Pope and Pope, 1949, in their study, and our counts essentially agree), 45 glutinosus from the Coastal Plain of Virginia and North Carolina (figure 15), 115 specimens of P. j. jordani (figure 16), 27 specimens of P. j. shermani, 72 specimens of P. j. metcalfi, 53 specimens of P. j. mela-

ventris, 14 specimens of P. j. rabunensis, 29 specimens of P. j. teyahalee, and 44 specimens of P. j. unicoi. For a given size, the range of variation is quite similar for each form, although there is often a statistically significant difference in the variability and/or the ontogenetic rate of change in the different species. The data of Pope and Pope (1951) indicate that P. ouachitae has a similar range of variation in number of teeth as glutinosus and jordani, although the average number of teeth is slightly higher. The number of teeth in 60 P. wehrlei (figure 17) seems to be less than in the above forms, while Pope (1950) shows that P. yonahlossee than the above forms. 39 P. caddoensis, although small in size, have even more teeth than P. yonahlossee of the same size range (figure 18). Except between adult wehrlei and yonahlossee, or wehrlei and caddoensis, there is considerable overlap in the vomerine tooth counts of all the Eastern Large Plethodons, and even in the case of these, only adults can actually be distinguished on the basis of this character. It is true that large series of adults of species that differ greatly in size (e.g. P. g. glutinosus and P. j. metcalfi) will differ in average number of vomerine teeth, but this is mainly a reflection of the difference in size between the two forms. This character obviously cannot be used as an aid in identification, since specimens of the two species that are the same size will have similar vomerine tooth counts.

Several other supposed differences mentioned in the literature are not useful in determining relationships. All, except P. wehrlei, have a similar number of costal grooves (see table VI). Sexual dimorphism in size is present in several forms that have been critically studied. The type of lateral guanophore pigmentation varies

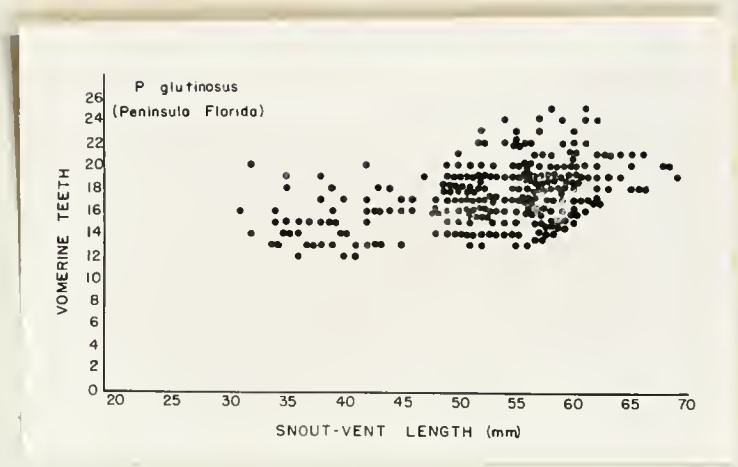

Figure 14. Vomerine teeth of 269 peninsula Florida P. glutinosus plotted against snout-vent length.

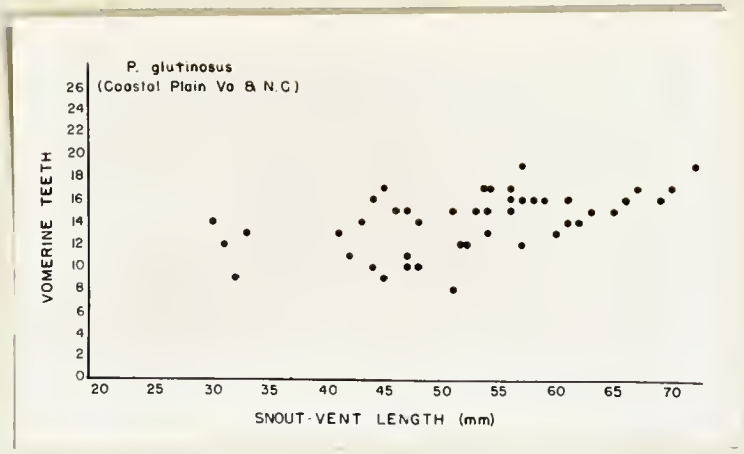

Figure 15. Vomerine teeth of 45 P. glutinosus from the Coastal Plain of Virginia and North Carolina plotted against snout-vent length.

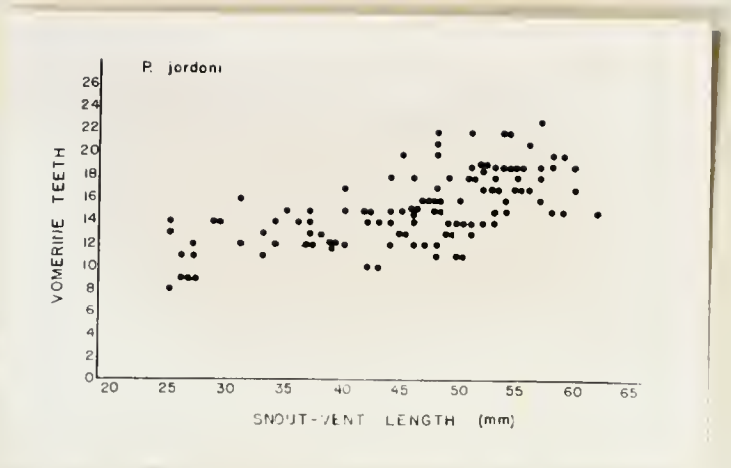

Figure 16. Vomerine teeth of 115 P. j. jordani plotted against snout-vent length.

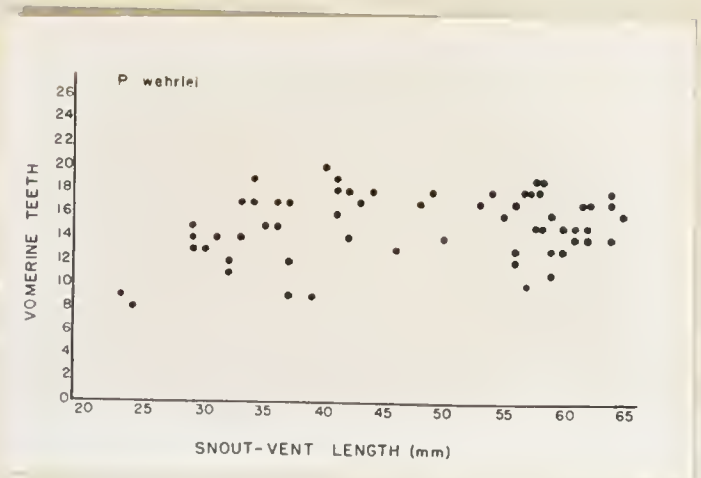

Figure 17. Vomerine teeth of 60 P. w. wehrlei plotted against snout-vent length.

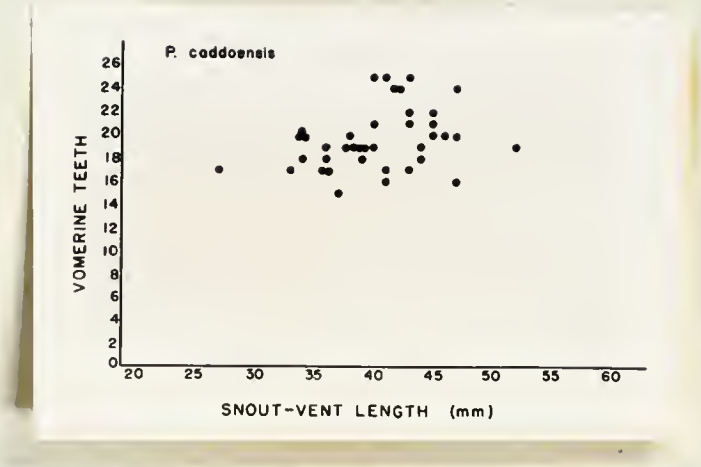

Figure 18. Vomerine teeth of 39 P. caddoensis plotted against snout-vent length.

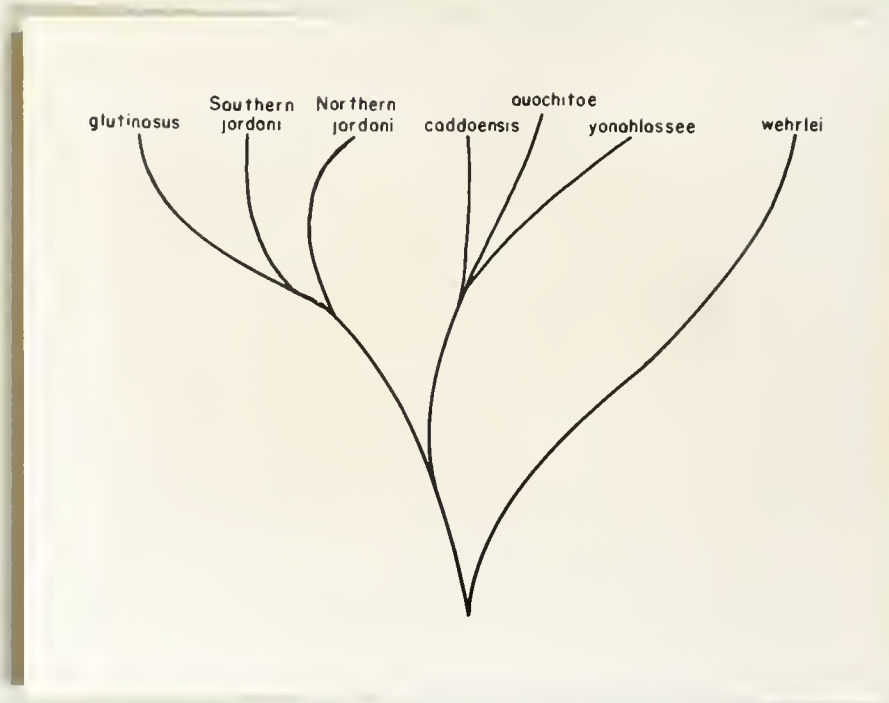

Figure 19. Suggested phylogeny of the Eastern Large Plethodons.

somewhat within a species (both individually and geographically), but there appear to be no consistant differences between species.

There remain, then, only a few characters that can be used to diagnose or distinguish the Eastern Large Plethodons. Each species is sympatric with, and often coexists in the same habitat with one or more of the other species without any evidence of interbreeding. As far as we know, each is a genetically distinct unit, and there is much evidence to indicate that different species have different ecological requirements. Yet preserved specimens that have lost their pigmentation characters are often extremely difficult to identify because of the morphological similarity of most of these salamanders.

P. wehrlei is distinguished on the basis of a greater amount of webbing on the toes, by having an average of one more trunk vertebra, and by possessing fewer vomerine teeth than the other species. P. yonahlossee may be recognized by its distinctive color pattern in life. It also differs from the others (except caddoensis) in possessing a greater number of vomerine teeth. P. ouachitae has a similar color pattern to that of yonahlossee, but it has fewer vomerine teeth. I have found no character that will consistantly separate glutinosus and jordani. The chin of glutinosus is usually darker than that of jordani, but certain populations of both species more closely resemble the other (some Texas glutinosus have very light chins, whereas P. j. teyahalee and some P. j. rabunensis possess dark chins). The close morphological similarity between all the forms, except P. wehrlei, indicate that they are a closely related group of species, with only wehrlei separated from the others by a number of characteristics.

TABLE VI

THE NUMBER OF COSTAL GROOVES AND VERTEBRAE IN THE EASTERN LARGE PLETHODONS

Form	No. of costal grooves			No. of trunk vertebrae			
	15	16	17	16	17	18	19
P. w. wehrlei[1]		3	57		2	48	
P. w. dixi						30	4
P. yonahlossee					12	2	
P. ouachitae					16		
P. caddoensis					35	2	
P. glutinosus[2]	32	319	14	19	212	15	
P. j. jordani	11	68	3		8	1	
P. j. metcalfi	10	78	2				
P. j. shermani	6	64	3		1		
P. j. unicoi	4	56	1				
P. j. melaventris	5	67					
P. j. rabunensis	1	39			6		
P. j. teyahalee	2	24	4				

1 This is the only form in the table in which the same specimens were used to count both costal grooves and trunk vertebrae. The data on both characteristics are included only to show the close correspondence between the two counts. No other specimen of any of the forms listed in the table was included under both costal grooves and trunk vertebrae.

2 For a geographic breakdown of these counts, see table VIII.

The young of yonahlossee, some wehrlei, and two races of jordani are known to possess dorsal red spots. These disappear in adult wehrlei (except P. w. jacksoni) and jordani, and become incorporated into the dorsal red stripe of yonahlossee. No information is yet available on the very small young of ouachitae, caddoensis, and several of the races of jordani, but young ouachitae may possess them (see Pope and Pope, 1951: 145). The red dorsal spots appear to be definitely absent in the young of glutinosus. Red pigment was absent in all of the newly hatched young I have examined from Florida (Highton, in press), as well as in very young specimens from many other localities. Dunn (1926: 139) records a specimen of P. glutinosus from Clayton, Georgia, that had tiny paired red dorsal spots, but this may well be a specimen of P. j. shermani, known to occur within 10 miles of Clayton. Cope (1889: 141) also records young specimens of glutinosus from caves in Montgomery County, Virginia, possessing these spots, but the specimens were probably P. w. jacksoni.

A reduction in the amount of melanophore pigmentation on the chin occurs in yonahlossee, ouachitae, caddoensis, wehrlei, most races of jordani (except teyahalee and some rabunensis) and in some Texas glutinosus (albagula).

Most species possess a dark belly, but the four northern races of jordani (jordani, shermani, unicoi, and especially metcalfi) are light-bellied, as are some southern wehrlei.

P. yonahlossee and P. glutinosus (except for its southeastern Coastal Plain representatives) attain a larger maximum size than the

other species. P. caddoensis appears to be the smallest Eastern Large Plethodon. P. j. metcalfi might also be considered a dwarfed form.

Red pigment occurs in adult jacksoni, yonahlossee, ouachitae, jordani, and shermani. Dorsal guanophores occur in glutinosus, albagula, ouachitae, caddoensis, clemsonae, and teyahalee. Lateral guanophores are usually present in all Large Eastern Plethodons, except for four races of jordani (jordani, metcalfi, melaventris, and some shermani).

In summary, P. wehrlei seems to be the most distinct of the Eastern Large Plethodons, while the others seem to be morphologically very similar to each other. In my opinion, the hypothetical ancestor of the group might most reasonably be assumed to have been a moderate-sized animal with a light chin and dark belly, probably with paired red spots on the dorsum of the adult, possessing 17 trunk vertebrae, a short vomerine series, and webbed toes. P. wehrlei is closest to this hypothetical ancestor, although its body has become slightly elongated with the addition of an extra trunk vertebra. The chin is still light in all except glutinosus (albagula excepted) and one or two races of jordani. The dark belly has remained in all but the four northern races of jordani and in southern wehrlei. A larger size has been attained by yonahlossee and glutinosus, while dwarfing has occurred in northern jordani (especially metcalfi) and caddoensis. P. yonahlossee has a much longer vomerine series than the others. The degree of relationship indicated by a study of these characters would seem to indicate a phylogeny as outlined in figure 19.

Plethodon wehrlei Group

Plethodon wehrlei

Plethodon wehrlei inhabits the unglaciated Appalachian Plateaus Province in southwestern New York, western Pennsylvania, extreme southeastern Ohio, West Virginia, and adjacent Virginia (where it occurs a short distance outside the Appalachian Plateaus Province). This species is the most distinct of the Eastern Large Plethodons and appears to occupy a somewhat isolated position in the group, differing from the other species in several respects. There is usually more webbing on the toes of this species, although occasional specimens of other species, especially P. caddoensis and P. ouachitae, approach P. wehrlei in this regard. P. wehrlei is the only Eastern Large Plethodon that normally has 18 trunk vertebrae; all the others usually possess 17. P. wehrlei possesses fewer vomerine teeth than any other Eastern Large Plethodon and it is the only species that has melanophore pigmentation in the peritoneum.

Two close relatives of Plethodon wehrlei from southwestern Virginia (P. dixi and P. jacksoni) have recently been described as distinct species by Pope and Fowler (1949) and Newman (1954). P. dixi appears to differ from P. wehrlei only in proportions and pigmentation. It would seem best to regard it as a subspecies of P. wehrlei, since it replaces the latter geographically. P. jacksoni, based on specimens from an adjacent county, less than 15 miles from the dixi localities, essentially differs from P. wehrlei in the retention of the juvenile dorsal red spots in the adult. Young West Virginia wehrlei often possess these spots, but they appear to be absent in more northern wehrlei.

Since jacksoni does not otherwise differ from some wehrlei and dixi, it is also here regarded as a subspecies of P. wehrlei.

Several writers have commented on the geographic variation in P. wehrlei. Netting (1936: 91) lists ways in which West Virginia P. wehrlei differ from topotypic Pennsylvania specimens. The former possess white spotting on the throat and chest, while in Pennsylvania specimens the white spotting is absent. The lateral white pigment is also more abundant in West Virginia material.

Dunn (1926: 135) mentions the presence of paired red spots on the dorsum of a juvenile from Bristol, West Virginia. Brooks (1945: 231) reports that three adults, as well as most of the juveniles, in a series of 22 specimens from Randolph County, West Virginia, also possess dorsal red pigment. Bishop (1941: 238) states that none of the specimens of this species he has examined (presumably all from New York and Pennsylvania) have shown the slightest trace of red pigment.

Grobman (1944: 287) has pointed out some of the above differences between West Virginia and New York and Pennsylvania specimens, and has also suggested that southern wehrlei may attain a greater size than northern specimens. In view of these differences in northern and southern P. w. wehrlei, this form should be further studied for other evidences of geographic variation. It is possible that the northern and southern populations should be recognized as distinct subspecies. In the possession of reduced black pigmentation on the anterior portion of the belly, southern wehrlei are more similar to dixi and jacksoni than are northern wehrlei. In the presence of red spots on juveniles, as well as in some adults, West Virginia specimens are similar to

jacksoni. The increased lateral white pigmentation in southern wehrlei is also paralleled by jacksoni and dixi.

I have not carefully examined the pigmentation of any of the races of wehrlei in life, although a casual examination of living specimens from New York, West Virginia, and Virginia (dixi topotypes) was made before the present study was contemplated. A comparison of the geographic variation in pigmentation characters within the species, as well as with other Plethodons is much to be desired. Pope and Fowler (1949: 1) state that both "bronzy mottling" and "small light flecks" are present on the back of dixi. The former disappear rapidly in preservatives whereas the latter remain, although fading somewhat. Pope and Fowler state that they have occasionally observed the "white flecking" in wehrlei, but never the "bronzy mottling." The white flecking is probably the same type of spot evident on the specimen figured by Bishop (1941a: fig. 45). The red dorsal spots, present in young West Virginia wehrlei, were not observed by Pope and Fowler in a large series of paratypic dixi, including 59 juveniles. The belly of dixi is mottled (presumably with white guanophores on a melanophore background), whereas the belly of wehrlei is usually uniformly pigmented with melanophores. In size, dixi appears to be smaller than the other races. The specimens of dixi that have been examined also appear to have proportionately narrower heads and slenderer bodies than wehrlei.

Newman (1954: 12) states that the dorsum of jacksoni has "white flecks" and "silvery mottling," the latter usually disappearing within twenty-four hours after preservation. Mottling on the belly is also present, as in dixi. According to Newman, the dark belly pigmentation

fades in preservatives. Since some adult wehrlei from West Virginia have been reported with red spots on the dorsum, it may be found that these wehrlei and jacksoni are very similar, if not the same form. If this were the case, the name jacksoni would be available for southern wehrlei, should the latter be shown to be a distinct subspecies (see above).

A search should be made for P. w. dixi in southwestern Virginia, for it is very unlikely that it is restricted to the vicinity of two caves only two miles apart. Populations from other localities will be important in determining the amount of variation in the form, as well as its relationships with jacksoni and wehrlei.

Plethodon wehrlei wehrlei Fowler and Dunn

Plethodon wehrlei Fowler and Dunn (1917: 23-4). Dunn (1926: 133-6). Bishop (1927: 117-8). Hassler (1932: 95-6). Walker (1933: 224). Netting (1936: 89-93). Netting (1936: 28-30). Bishop (1941a: 232-9). Lachner (1942: 263). Bishop (1943: 281-4). Grobman (1944: 285-7). Brooks (1945: 231). Netting (1946: 12). Netting, Green, and Richmond (1946: 157-60). Brooks (1948: 244). Grobman (1949: 136). Newman (1954: 13).

Type:- ANSP 19123, collected at Two Lick Hills, Indiana County, Pennsylvania, in September, 1911, by R. W. Wehrle.

Diagnosis:- An Eastern Large Plethodon with webbing between the toes on the hind foot often extending to the joint between the first and second phalanges; 18 trunk vertebrae; and a lower number of vomerine teeth (4-11 in a single series) than in other Eastern Large Plethodons. Dorsal

red pigment is usually absent in adults, and white pigment is usually absent from the belly, except on the chin and between the anterior limbs.

Range:- From Allegany State Park, Cattaraugus County, New York, south in the Allegheny Plateau Section of the Appalachian Plateaus Province through western Pennsylvania and West Virginia, except for the southwestern portion of the latter state (figure 20). Also recorded from Monroe and Washington Counties, Ohio, by Walker (1933: 224), and from the Valley and Ridge Province of Highland County, Virginia, by Netting, Green, and Richmond (1946: 157). A specimen from the Blue Ridge Physiographic Province of Nelson County, Virginia, is questionably referred to this species by Grobman (1949: 136).

Description:- The pigmentation of this form has not been studied in life. Several writers have mentioned that this species is brown or bluish in appearance, probably an indication of a reduction in the intensity of melanophore pigmentation, as often occurs in the Eastern Small Plethodons. (The distinction between two types of guanophores on the dorsum given in the original descriptions of dixi and jacksoni are also reminiscent of the Eastern Small Plethodons.) Lateral guanophore spots are present on the sides, as well as on the chin of southern wehrlei. The young and occasional adults from West Virginia possess paired red dorsal spots (Brooks, 1945: 231).

The costal grooves usually number 17, the trunk vertebrae, 18. Vomerine teeth range from 4 to 11 in a series. This form is moderate in size, the largest specimens are about 70 mm. in snout-vent length.

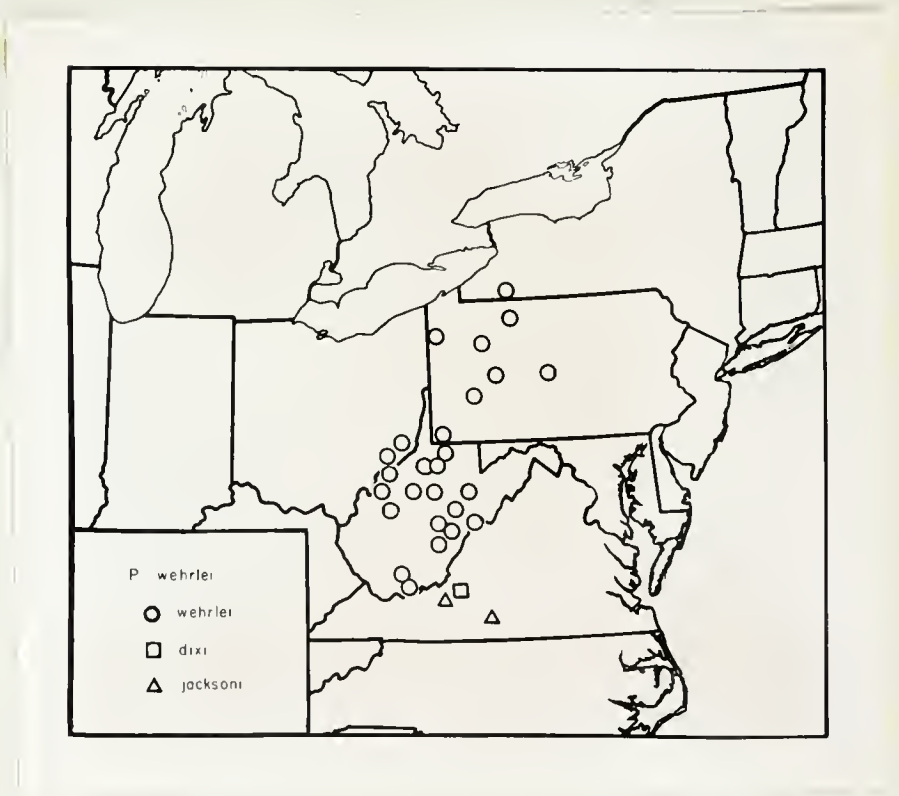

Figure 20. The distribution of the subspecies of Plethodon wehrlei.

Plethodon wehrlei dixi Pope and Fowler

Plethodon dixi Pope and Fowler (1949: 1-4). Fowler (1951: 147-8).

Type:- CNHM 56510, a male, collected at Dixie Caverns, Roanoke County, Virginia, on July 11, 1948, at an altitude of 1170 feet, by John W. Funkhouser, Sarah H. Pope, Clifford H. Pope, Hallowell Pope, and Whitney Pope.

Diagnosis:- Similar to P. w. wehrlei, except for slightly smaller size, slenderer head and body, the presence of white guanophore mottling on the belly, and small brassy flecks on the dorsum.

Range:- Known only from Dixie Caverns, New Dixie Caverns (about 440 yards from Dixie Caverns), and Blankenship Cave (about 2.4 miles east of Dixie Caverns), in western Roanoke County, Virginia (figure 20).

Description:- For a description of the type series in life, see Pope and Fowler (1949).

The costal grooves usually number 17, the trunk vertebrae, 18. Vomerine teeth range from 4 to 9 in a series. The largest specimen measured by Pope and Fowler was 57 mm. in snout-vent length.

Plethodon wehrlei jacksoni Newman

Plethodon jacksoni Newman (1954: 9-14).

Type:- An adult male, collected at Trillium Vale, about 1 mile east of Blacksburg, Montgomery County, Virginia, at an elevation of 2100 feet, on February 11, 1950, by Walter B. Newman.

Diagnosis:- Similar to P. w. wehrlei, except that the juvenile coloration, paried red dorsal spots, is retained in the adult.

Range:- Known from the vicinity of Blacksburg, Montgomery County, Virginia, and Smith Mountain Gorge, Pittsylvania County, Virginia (figure 20). The latter record extends the range of Plethodon wehrlei into the Piedmont Physiographic Province.

Description:- Specimens of this form have not been examined and no information other than that published in the original description is available.

Plethodon yonahlossee Group

Most previous workers have believed that this group is very closely related to P. wehrlei and it has even been suggested (Grobman, 1944: 276) that yonahlossee and wehrlei may eventually be shown to be subspecifically related. For reasons given above, it is suggested here that the yonahlossee group is actually more closely related to the glutinosus group than either is to the wehrlei group. The three species included in the yonahlossee group, yonahlossee, ouachitae, and caddoensis, appear to differ from the glutinosus group mainly in pigmentation characters. There are no other known consistant differences between the two groups, although there is variation in size and other characters within each group.

The disjunction in the ranges of the species of this group suggests that the prototype was once widely distributed in the eastern United States, and that due to subsequent environmental changes, the

three populations have become isolated. In external appearance, at least, yonahlossee is quite similar to ouachitae. P. caddoensis, occupying an area adjacent to ouachitae, appears quite distinct from both ouachitae and yonahlossee. This would seem to indicate that the two species, caddoensis and ouachitae, have been undergoing differentiation west of the Mississippi River for quite some time. Pope and Pope (1951) have suggested that there may be two other undescribed forms of this group in Oklahoma and Arkansas.

P. yonahlossee is most abundant at intermediate altitudes in the southern Appalachians, being rare or absent in the northern-type spruce-fir forests as well as at low altitudes below 2500 feet (Pope, 1951: 81). In Arkansas and Oklahoma, P. ouachitae is known from 1700 to 2800 feet on Rich Mountain, while P. caddoensis has been taken at lower elevations, from 950 to 1200 feet. Both P. ouachitae and P. yonahlossee occur in abundance at localities where P. glutinosus is also present, so it would appear that the two are able to coexist with P. glutinosus under certain conditions. It would therefore seem most likely that factors other than competition with glutinosus are responsible for the absence of the P. yonahlossee group at lower altitudes in the eastern United States. Possibly the higher temperatures existing at lower elevations are important factors in restricting the present distribution of these forms, but so little is known about the life history, physiology, and ecological requirements of these animals that it is useless to speculate further on these matters.

In several ways the yonahlossee group appears somewhat closer to P. wehrlei than do the members of the glutinosus group. For example,

some caddoensis and ouachitae possess toes which are slightly webbed, approaching the condition in wehrlei. The presence of red dorsal spots in the young of yonahlossee (and possibly ouachitae) are similar to those in the young of southern wehrlei (but these are also present in the young of two members of the glutinosus group, jordani and shermani). On the other hand, all three species in the yonahlossee group have an average of more vomerine teeth than both wehrlei and the glutinosus group, and all three resemble the glutinosus group in possessing 17 trunk vertebrae, as opposed to the 18 of wehrlei. It is apparent that no one species in the yonahlossee group is closer to wehrlei than any of the others. Thus, it would seem that, as a group, their relationship to wehrlei is quite remote.

The knowledge of the three species in this group has recently been summarized and augmented by two excellent papers by Pope (1950) and Pope and Pope (1951). Little new information on variation, ecology, and life history, other than that already discussed, can be offered here.

Grobman (1944: 278) has discussed the relationship between ouachitae and yonahlossee and suggested the need for further morphological as well as experimental studies to determine whether the two should be considered separate species, different subspecies, or undifferentiated populations of the same species. The work of the Popes has demonstrated that these forms differ in size at maturity, maximum size, coloration, and in the number of vomerine teeth, although there is some overlap between the two in the last two mentioned characters. Consequently, they are certainly not undifferentiated populations of

the same species. Whether to consider them different species or subspecies is more difficult to determine. The differences between them appear, however, to be as great or greater than those between other distinct species in the genus (e.g. jordani and glutinosus; cinereus and dorsalis; or dunni and vehiculum). It would seem best to continue to regard them as separate species. Pope and Pope (1951: 149) suggest that the relationship between caddoensis and ouachitae might be subspecific, but the differences in vomerine teeth, size, and color pattern would appear to indicate that they, too, have reached the species level of differentiation. The three might appropriately be called a superspecies (Mayr, 1931: 2).

Plethodon yonahlossee Dunn

Plethodon glutinosus (Green). Brimley (1912: 137-8)

Plethodon yonahlossee Dunn (1917: 598-603). Dunn (1920: 130-1). Breder and Breder (1923: 15). Dunn (1926: 129-33). Bailey (1937: 2-3). Gray (1939: 106). Bishop (1943: 287-90). Grobman (1944: 287). Wood (1947: 273-4). Hairston and Pope (1948: 276-7). Hairston (1949: 53-6). Pope (1950: 79-105). Newman (1954: 13).

Type:- AMNH 4634, collected near the Yonahlossee Road, about 1½ miles from Linville, Avery County, North Carolina, at an altitude of 4200 feet, on August 16, 1916, by E. R. Dunn and W. S. Nevin.

Diagnosis:- A large species, with paired dorsal red spots in the young, and a dorsal chestnut-colored stripe in the adult. Guanophores lacking in the region of the dorsal stripe, but concentrated on the sides to form a white or light gray lateral band.

Range:- Northeast of the French Broad River in the Blue Ridge Province of North Carolina, Tennessee, and southeastern Virginia (figure 21). Pope (1950: 82) mentioned that this species had never been found east of the New River in Virginia, but more recently, Newman (1954: 13) reported two specimens from Kibler Park, Patrick County, Virginia. It may eventually be found farther north in the Blue Ridge Province in Virginia (Floyd and Franklin Counties).

Description:- The belly is black with few to many small white spots. The throat is usually light. The dorsal chestnut-colored stripe is made up of both red and black pigment. The red pigment appears to be somewhat similar to the red pigment of jordani and shermani, but the additional presence of black pigment gives the animal its characteristic chestnut-colored dorsum, rather than the bright red of the other forms. The black pigment is concentrated around the mucous glands in the skin. The young possess paired dorsal red spots and these often remain evident after several years of preservation, unlike the chestnut band of the adults. The reason for this appears to be the absence of melanophores in the red spots of the young, so that when the red pigment dissolves in the preserving fluid, a light melanophore-free "spot" remains. In the adult, the melanophores occur over the entire back, so when the red pigment disappears, the animal appears black. Occasional specimens have a reduced amount of red pigment on the dorsum in life, and one specimen reported by Pope (1950: 97) lacked the dorsal red pigment completely. The lateral guanophore pigmentation is so concentrated that in most individuals it forms a light gray or white lateral band.

Figure 21. The distribution of the Plethodon yonahlossee Group.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 5 to 22 in a series, a greater number than in any other Plethodon. The largest specimen examined by Pope (1950) was a female, 85 mm. in snout-vent length. Sexual maturity is apparently reached between 55 and 65 mm. in snout-vent length.

Plethodon ouachitae Dunn and Heinze

Plethodon ouachitae Dunn and Heinze (1933: 121-2). Bishop (1943: 269-72). Grobman (1944: 285). Pope and Pope (1951: 129-52).

Type:- USNM 92484, an adult male, collected on the north side of Rich Mountain, Polk County, Arkansas, on May 30, 1933, by Albert A. Heinze and Dorothy A. Boyer.

Diagnosis:- A moderate-sized species with a dorsal chestnut-colored stripe as in yonahlossee, but with numerous white spots and brassy flecks on the back, that are not present in yonahlossee. The lateral band is often yellow in color, whereas in yonahlossee it is usually white or very light gray.

Range:- Known only from Rich Mountain in Polk County, Arkansas, and LeFlore County, Oklahoma (figure 21). Also reported by Dundee (1947: 118) from McCurtain County, Oklahoma, but Pope and Pope (1951: 134) present arguments that the specimen on which this record is based is not ouachitae, but an undescribed form.

Description:- The variation in over a hundred specimens of this species has been studied by Pope and Pope (1951). I have examined only three living specimens of this species, so reference is made to their paper

for the frequency of the occurrence of pigmentation characters.

The belly is dark. The intensity of melanism on the chin is variable, ranging from very dark in a small percentage of specimens to little evident or lacking in 27%. 93% of the Popes' specimens possessed yellow or white spots on the chin and over half possessed these spots on the belly.

Lateral white or yellow pigment is so abundant on the sides that in 85% of the specimens it forms a continuous band.

The back has four different types of chromatophores. Black pigment is present on the dorsum and is concentrated around the glands in the skin, as in yonahlossee. Between these glands there is a fairly uniform amount of red pigment. In addition there are two kinds of guanophores scattered over the dorsum. There are small white spots (the "white speckling" of Pope and Pope) and smaller brassy flecks (their "frosting"). The white spotting was lacking in 2% of their specimens and the brassy flecks were lacking in 19%. There was considerable variation in the abundance of both types of guanophores. There is also a great deal of variation in the amount of red on the back. In 21% of their specimens they state that the back was nearly all black.

After preservation, a 26 mm. juvenile exhibited two rows of faintly pink spots on the back, indicating that this form may have the juvenile red spots present in several other Eastern large Plethodons.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 4 to 18 in a series. The largest specimen,

a female, is 67 mm. in snout-vent length. Sexual maturity is apparently reached between 45 and 55 mm. snout-vent length.

Plethodon caddoensie Pope and Pope

Plethodon ouachitae Dunn and Heinze. Grobman (1944: 285, part).
Plethodon caddoensis Pope and Pope (1951: 148).

Type:- CNHM 61959, a female collected at an altitude of 1200 feet on Polk Creek Mountain, Montgomery County, Arkansas, by Sarah H. Pope, on May 9, 1950.

Diagnosis:- A small species with melanophore pigmentation almost entirely absent on the chin and belly anterior to the fore-legs. Dorsal spots are larger and more numerous than in P. glutinosus. It possesses an average of more vomerine teeth for its size range than any other Plethodon. The toes are often slightly webbed at the base.

Range:- Known only from the Caddo Mountains of southern Montgomery County, Arkansas (figure 21).

Description:- This species has not been examined in life and little more can be offered than that already discussed. Pope and Pope (1951) give a description of the holotype and two paratypes in life.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 7 to 14 in a series. This is a small species, the largest specimen of 39 examined is 52 mm. in snout-vent length. Sexual maturity is reached at about 40 mm. snout-vent length. Pope and Pope believed that all three of their specimens were immature, although two of these were 45 and 47 mm. in snout-vent length.

Plethodon glutinosus Group

Plethodon jordani

In 1901, Blatchley described a red-cheeked Plethodon from the Great Smoky Mountains as Plethodon jordani. During the next three decades, three additional related forms were described by Stejneger (1906) and Brimley (1912, 1927) as separate species, although each was obviously closely related to P. jordani and inhabited an adjacent region. Both Dunn (1926: 146; 151) and Grobman (1944: 289) commented on the close relationship of these forms and suggested that intergrades between some of the adjacent forms might eventually be found. Brimley also recognized their close relationship and mentioned that "they hardly seem distinct enough to be full species"(1928: 23). The studies of Hairston and Pope (Hairston and Pope, 1948; Pope and Hairston, 1948; Hairston, 1950) added three new forms to the group and demonstrated that intergradation occurs between several adjacent forms. In 1950, Hairston recognized seven subspecies of P. jordani, and another supposed member of this group (P. kentucki) was described by Mittleman as a distinct species in 1951. It was later listed as a subspecies of Plethodon jordani by Schmidt in 1953, but Clay, Case, and Cunningham (1955) have shown that the specimens on which it was based are actually P. glutinosus.

In spite of the fact that much has been learned about the systematics of this group during recent years, there still remain numerous gaps in the knowledge of the distribution and relationships of many of the forms, some of which have heretofore been recorded only from a single type locality. During the summer of 1955, I had an op-

portunity to spend several weeks collecting in the southern Appalachians and a special effort was made to obtain salamanders of this group from several critical areas. In addition, a large number of plethodons of this species in the University of Florida collection, assembled since 1951 by Dr. Arnold B. Grobman, Walter Auffenberg, Edwin H. McConkey, the writer, and others, were available for study. This new material has demonstrated the close relationship of certain members of the jordani group with Plethodon glutinosus, as well as providing information on the relationships among the several subspecies. In addition, one new form was discovered. Recent collecting outside the southern section of the Blue Ridge Province, in which these salamanders were formerly believed to be largely restricted, has indicated that some of the forms may have more extensive distributions (Hoffman and Kleinpeter, 1948; Hoffman and Hubricht, 1954). With the continued building of roads into previously poorly accessible areas of the southern Appalachians, opportunities for additional profitable studies with this group are increasing.

Careful color notes from life were made on the specimens I collected during the summer of 1955 and the entire collection was critically examined, after preservation, in September, 1955.

Each series was studied in order to determine whether it could be assigned to either the light-bellied or the dark-bellied group of subspecies. The importance of the difference in intensity of ventral melanophore pigmentation has been emphasized by Bailey (1937), Grobman (1944), Hairston and Pope (1948), and Hairston (1950), as an important character in the study of raciation in this species. The subspecies

jordani, melaventris, clemsonae, rabunensis, and teyahalee were regarded as dark-bellied races, while metcalfi and shermani were described as being light-bellied. No one has offered an explanation for the discontinuous distribution of the light-bellied populations. The new material that has been collected in the last five years indicates, however, that several other populations of Plethodon jordani are light-bellied. These occur in the northern Cowee Mountains (a range lying between the Nantahala Mountains inhabited by P. j. shermani and the Balsam Mountains inhabited by P. j. metcalfi); in the Unicoi Mountains (this population will be described as a new subspecies, P. j. unicoi, below); and in the Great Smoky Mountains.

In order to study the intensity of ventral melanophore pigmentation in an objective manner, the freshly preserved specimens collected during the summer of 1955 were compared with a standard color guide (Villalobos and Villalobos, 1947) and the degree of darkness of the belly recorded. Since immature specimens of all the forms have much lighter bellies than adults, only the variation in sexually mature individuals was studied. Table VII shows the data on this character obtained from specimens taken in various parts of the range of Plethodon jordani. It is obvious that there is considerable variation in the darkness of the bellies of specimens in each population. However, with the exception of P. j. jordani, the forms considered to be dark-bellied by previous workers, do average darker than those which were considered to be light-bellied. P. j. jordani should actually be considered a light-bellied subspecies, since the average belly pigmentation is well within the range of the other light-bellied races (shermani and metcalfi). The distinction between light- and dark-bellied populations is not ab-

TABLE VII

THE INTENSITY OF VENTRAL MELANOPHORE PIGMENTATION OF FRESHLY PRESERVED SAMPLES OF THE SUBSPECIES OF PLETHODON JORDANI, BASED ON READINGS TAKEN WITH THE COLOR ATLAS OF VILLALOBOS AND VILLALOBOS (1947). LOWER READINGS INDICATE DARKER BELLIES AND HIGHER READINGS INDICATE LIGHTER BELLIES. ONLY SEXUALLY MATURE INDIVIDUALS ARE INCLUDED IN THE TABLE IN ORDER TO MINIMIZE ONTOGENETIC VARIATION.

Sample	Grayness Readings										Mean
	5	6	7	8	9	10	11	12	13	14	
Plethodon j. jordani											
Gregory Bald				1	3	2	1	2	1		10.3
Spence Field					1	1	2	1	2	1	11.6
Indian Gap		3	16	19	22	19	7	2	1		8.8
Mt. Sterling			1	5	2	2					8.5
Spruce Mountain			2	2	1						7.8
Plethodon j. jordani x metcalfi											
Chiltoskie Ridge				1	1	2					9.3
Plethodon j. metcalfi											
Soco Gap and Heintooga Ridge			1	1	3	3	2		1		9.7
Max Patch					1	1	1				10.0
Cowee Bald					1					2	12.3
Crest of Balsam Mountains (between Beech Gap and Mt. Pisgah)			1	5	5	7	1	1			9.3

TABLE VII (CONTINUED)

Sample	Grayness Readings 5	6	7	8	9	10	11	12	13	14	Mean
Plethodon j. metcalfi (continued)											
Northeast of French Broad River			1	2	5	4	4	1			9.6
Plethodon j. shermani											
Tellico Gap		1									6.0
Wayah Bald				2	1		2				9.4
Black Gap				1	4	4	1				9.5
Mooney Gap				2	3	2	1	1			9.6
Plethodon j. unicoi											
Unicoi Mountains		1	2	5		2		1	1		8.8
Plethodon j. melaventris											
Highlands	12	25	6	3							6.0
Plethodon j. rabunensis x melaventris											
Rabun Bald		5	5	2							6.8
Plethodon j. teyahalee											
Teyahalee Bald		2	2								6.5
Junaluska Gap		1	1	4							7.5

solute, but is only an average difference that can be detected by examining series of freshly preserved specimens. Nine living adult specimens from Grandfather Mountain (metcalfi) are almost as dark as preserved melaventris (range, 5-9; mean, 7.0), and 21 living adult melaventris are slightly darker (range, 2-7; mean 4.7). Again, an average difference exists, but living specimens cannot be compared with preserved specimens, and probably additional fading may be expected after several years of preservation. Different preservatives probably give rise to other variations in amount of fading.

A series of ten living specimens of metcalfi from Grandfather Mountain and ten living melaventris from Highlands were both separated into two groups of five each and one was kept in light and the other in dark conditions for eight days. At the end of this period, the four groups did not appear to have changed detectably in the intensity of their melanophore pigmentation. In a similar experiment, Grobman (1950) found that the belly pigmentation of light- and dark-bellied races of Desmognathus fuscus was subject to changedin intensity when exposed to different light conditions.

The distribution of the light- and dark-bellied populations of Plethodon jordani can now be reexamined in the light of these new data. If populations averaging 7.5 or under are considered dark-bellied and those over 7.5 light-bellied, it can be seen from figure 22 that the light-bellied populations (jordani, metcalfi, shermani, and unicoi), represented by hollow symbols, are not isolated from one another by intervening dark-bellied populations, as was formerly believed. If populations that average 8.0 and over, or 8.5 and over are considered light-bellied, and the remainder dark-bellied, the results would be

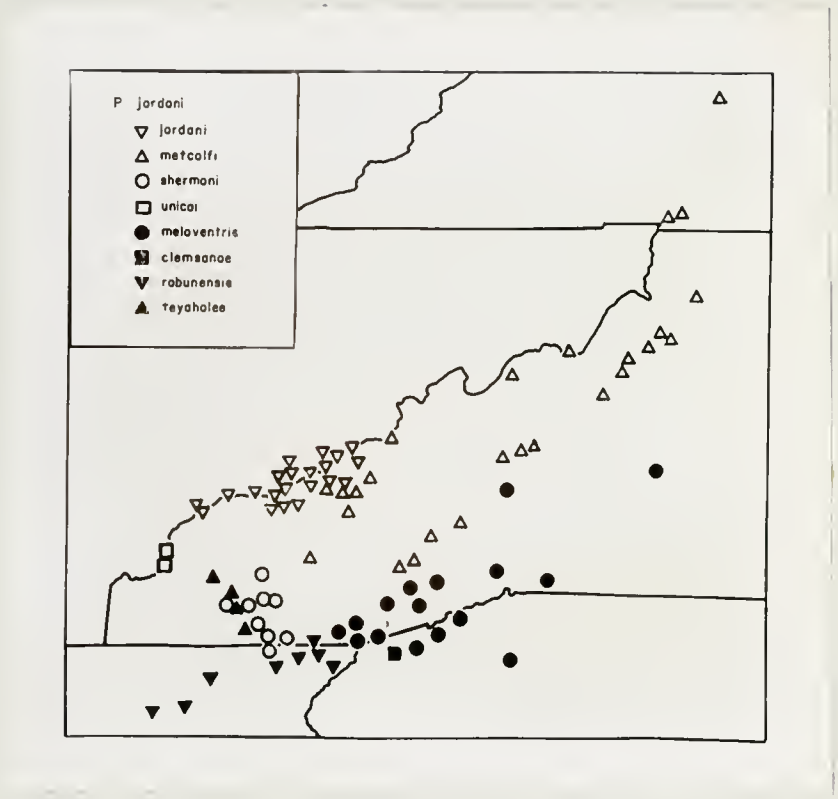

Figure 22. The distribution of the subspecies of Plethodon jordani. Solid symbols represent dark-bellied races and hollow symbols represent light-bellied subspecies.

similar. If a lighter dividing line were used, then some races here considered light-bellied would include both types. The dark-bellied populations (melaventris, rabunensis, clemsonae, and teyahalee), indicated by solid symbols in figure 22, apparently occur in the southern portion of the range of Plethodon jordani.

Most previous workers were convinced that the subspecies of Plethodon jordani were either isolated in the present mountain ranges or in the valleys between them during former periods of different climatic conditions (see Hairston, 1950, for a discussion of this problem). The present distribution of the races of Plethodon jordani does not necessarily support either of these views. P. j. metcalfi, for example, occurs in several different mountain ranges (Black, Balsam, Cowee) that are separated by low uninhabited river valleys. It intergrades with P. j. jordani at high altitudes in the northern Balsam Mountains. On the other hand, it is separated from P. j. shermani by the valley of the Little Tennessee River. P. j. shermani occurs on both sides of the Nantahala River, although a few miles west of the river it is replaced by P. j. teyahalee. P. j. melaventris and P. j. rabunensis intergrade in the vicinity of Rabun Bald, the highest elevation between the ranges of the two races. It is apparent that some races are separated by river valleys, while others are separated by mountain ranges. Intergradation usually occurs in the mountain ranges where two forms come together, but cannot occur in some of the deep valleys that are presently ecologically unsuitable to members of this species. River valleys and high mountain ranges may thus both serve as barriers between pairs of different subspecies, and both appear to be factors important in the present distribution of the subspecies of

P. jordani.

The first differentiation that occured in P. jordani was probably a separation of the proto-jordani stock into a northern light-bellied form and a southern dark-bellied form. It is useless, at this time, to speculate when or how this occurred, since we have no idea of the geologic age of the species concerned. Later, each of these forms developed four restricted groups that can be recognized today as separate subspecies. During the Pleistocene, climatic changes were frequent, and it is quite possible that at different times both river valleys and mountain ranges acted alternately as routes of dispersal and barriers to migration.

The differences between the two major groups of races are not limited to belly pigmentation alone. The northern races are smaller and show a more marked sexual dimorphism in the swelling of the snout in males. Dorsal guanophores are absent in the northern light-bellied forms, although present in several populations of the southern group (clemsonae and teyahalee). Lateral guanophores are present in both groups, but are most abundant in the southern populations, especially rabunensis. Red lipophores appear in shermani and jordani and occasionally in other populations, especially those adjacent to shermani. The northern races are restricted to higher altitudes, whereas the southern dark-bellied races occur at low altitudes (under 3500 feet) as well. The southern forms are morphologically much more similar to glutinosus, and the two species often coexist in the same habitat, while the northern, light-bellied forms are usually altitudinally separated from P. glutinosus (Hairston, 1951).

The subspecies jordani and shermani are obviously closely related. Both forms have young that have similar red dorsal spots (Bailey, 1937: 5-6; Wood, 1947a, 1947b). Both have fairly light bellies and both possess red pigment as adults. Hairston (1950: 270) suggests that intergradation may have taken place between the two during the Pleistocene when the Little Tennessee River Valley might have been inhabited by the two. The Cheoah Mountains, which rise to over 5000 feet in elevation, lie directly between the Smokies and the Nantahalas and an intermediate population may be present there at this time. This area should certainly be searched for it probably supports a member of the jordani group. One might expect shermani, teyahalee, jordani, intermediates between any of these, or perhaps, a new form. Hairston (1950) reported intergrades between jordani and metcalfi, metcalfi and melaventris, and rabunensis and shermani. He is probably correct in suggesting that jordani and shermani are very closely related, rather than being circuitously connected through the subspecies metcalfi, melaventris, and rabunensis.

Hairston (1950) reports intergrades between jordani and metcalfi from Hyatt Ridge, a ridge that runs south from the vicinity of Mt. Guyot in the main Smoky Mountain chain. I have examined some of his specimens (GSMNP Pm 20-29) and agree with the interpretation that they are intermediate between the two forms. A series of 10 specimens from Spruce Mountain (GSMNP Pj 96; UF 8150), 7 miles east of Hyatt Ridge in the direction of the range of metcalfi, are typical jordani (except for one specimen that has a reduction of red pigment on one cheek). Four miles to the south of Spruce Mountain, at Heintooga Ridge, 15 specimens (UF 8121, 8250) all completely lack red pig-

ment on the cheeks. At Chiltoskie Ridge, about half way between these two localities, six specimens (UF 8147) are intermediate between jordani and metcalfi. Of these, one specimen has no red on the cheeks, another has normal jordani red cheeks, and the remaining four all have a very reduced amount of red on the cheeks. The zone of intergradation between the two forms on Balsam Mountain therefore appears to be very narrow (i.e. less than four miles). King (1939: 553) reports taking the two forms less than a mile apart without any evidence of intergradation. He does not give the exact location of his collections, but 15 specimens from Hyatt Ridge in the GSMNP collection (Pm 1-13, 3500'; Pm 14-15, 4080') all appear to lack any trace of red on the cheeks. Two specimens (GSMNP Pj 81-82) taken at 4500 feet on Hyatt Ridge, are fairly typical jordani. Unfortunately, no further locality data are available for any of these specimens, but they indicate that both fairly typical jordani and metcalfi, as well as intergrades between the two (see above), occur on Hyatt Ridge, the same situation that occurs on Balsam Mountain, the next ridge to the east.

King (1939: 551) reports that only two of several hundred specimens of jordani from the Smokies that he examined lacked red cheeks. There is, of course, considerable variation in the amount of red that occurs on the cheeks of jordani at the type locality in the center of its range where the incidence of red pigmentation reaches its greatest development. Some specimens have red extending across the gular region, shoulders, and even onto the fore limbs. Others have the red restricted to a part of the cheek only (usually the upper half). In examining the specimens of jordani in the GSMNP collection, I found only two that lacked any trace of red on the cheeks. One, Pj 22, is from Mt. Sterling

at the extreme east end of the Park, and the other, Pj 45, is one of two specimens with the same number. There is no specimen labelled Pj 54, so apparently an error has been made in tagging the specimens. Since Pj 45 and Pj 54 are from different localities (Hughes Ridge, and Long Hungry Ridge, respectively) some 33 miles apart, it seems best to disregard this record.

Two series collected by the writer during the summer of 1955, at Gregory Bald (UF 8125) and at Mt. Sterling (UF 8141), at opposite ends of the Park, both show a great reduction in the amount of red on the cheeks. None of the 33 specimens from Gregory Bald completely lack red cheek pigment, but 18 (67%) have less red on the cheeks than 138 of 141 topotypes examined from Indian Gap (UF 8094, 8141, 8254). The series from Gregory Bald may be tending slightly toward the new form, unicoi, in that several specimens have small white spots on the sides of the head and body. Of 14 specimens from Mt. Sterling, two entirely lack red cheek pigment, six have it greatly reduced, and six fall within the usual range of topotypes of jordani. The specimens from Mt. Sterling may be approaching metcalfi, which is known from two localities on the Cataloochee Divide (GSMNP Pm 16, Sugar Tree Lick; and UF 8144, Cove Creek Gap). Four specimens from Max Patch Mountain (UF 8135), on the east side of the Pigeon River, are typical metcalfi.

Specimens in the GSMNP collection from many localities in the central portion of the Smokies are all similar to topotypical jordani. Large series from single localities are not available, except from the type locality, so it is impossible to analyze populations from different areas in order to determine, to any further extent, whether or not

any trends in the reduction of red pigment on the cheeks and intensity of ventral melanophore development are present.

P. j. metcalfi has the most entensive range of any of the races of P. jordani. It occurs from the Cowee and Balsam Mountains in southwestern North Carolina to southwestern Virginia. The northern-most record for metcalfi in Virginia is Burkes Garden (Hoffman and Kleinpeter, 1948), a locality in the Valley and Ridge Physiographic Province. This race seems to be fairly uniform throughout its range. The fact that an isolated population of metcalfi occurs on Cowee Bald in the Cowee Mountains seems to indicate that there was a former connection across the present low Tuckasegee River valley with metcalfi populations in the Balsam Mountains. The Cowee Mountains range to the southeast into melaventris territory and thus do not connect directly with any other mountain range known to be inhabited by metcalfi.

The young of metcalfi have not been described. A special effort was made to obtain such specimens in order to ascertain whether or not they possessed the red dorsal spots of juvenile shermani and jordani. Only three young of the year were found, all from the vicinity of Mt. Pisgah, in southern Haywood County, North Carolina. None had any red pigment and two, both 19 mm. in snout-vent length showed no trace of guanophores either. The other specimen, 20 mm. in snout-vent length, had numerous guanophores scattered over the back and sides, unlike any adult metcalfi examined.

Hairston (1950) presents evidence for intergradation between metcalfi and melaventris in the southern Balsam Mountains. He compared specimens from both the northern and southern slopes of the Balsams in

the vicinity of Beech Gap, and found an apparent increase in darkness of the belly from north to south. Most light-bellied populations include specimens that are as dark as some melaventris or rabunensis (see table VII), but samples from the top of the Balsam Mountains; near Beech Gap (UF 8109), near Wagon Road Gap (UF 8108), and Mt. Pisgah (UF 8145) average only slightly darker than other samples of metcalfi. Intergradation between these two forms probably takes place to the south or southwest of the top of the Balsam Mountains in this area, not on the crest of the mountains. I have not examined freshly preserved or living material from any localities between Beech Gap and Highlands. Until such material is available from these areas, I would hesitate to assign subspecific identifications to the populations that exist in this area, as well as to those reported from Burke, Henderson, and Polk Counties, North Carolina, and from Greenville and Pickens Counties, South Carolina, by Grobman (1944), Hoffman and Hubricht (1954) and Schwartz (1953: 156; 1954), although these workers assigned specimens from these counties to the southern dark-bellied form (melaventris). These localities are tentatively indicated on the distribution map of these forms as melaventris (figure 22). The great difficulty in distinguishing preserved P. glutinosus and the southern dark-bellied races of P. jordani casts some doubt on the correct identification of some of the records of melaventris cited in the literature.

At high elevations in the Unicoi Mountains, at altitudes above 4000 feet, in the vicinity of Haw Knob and Johns Knob, a light-bellied population of P. jordani was discovered by Dr. Arnold B. Grobman in 1950. In the same year, Hairston described P. j. teyahalee, based on seven specimens from Teyahalee Bald in the nearby Snowbird Mountains.

The comparison of living topotypes of teyahalee with the form from the Unicoi Mountains reveals that the latter population is not teyahalee, but an undescribed form. It is distinguished from teyahalee by its lighter belly, the absence of small red spots on the legs and the usual absence of tiny white spots on the back. Its light belly also distinguishes it from rabunensis, melaventris, and clemsonae. The absence of red pigment distinguishes it from jordani and shermani, and the presence of lateral white or yellow spots distinguishes it from metcalfi. As noted above, specimens of jordani from Gregory Bald, in the extreme west end of the Great Smoky Mountains, show some tendency toward unicoi characters, and may represent intermediates between the two forms.

P. j. shermani, the red-legged form from the Nantahala Mountains, occupies an area extending from Tellico Gap, in the northern portion of these mountains, south to the vicinity of the Georgia state line. Bailey (1937: 5) records this race from the Tusquitee Mountains, indicating a geographic overlap of shermani and teyahalee (see below).

Hairston (1950) reports several series of dark-bellied shermani from the periphery of its range. One of these localities is Tellico Gap, in the northern Nantahala Mountains. Two fresh specimens (one of them immature) from this locality (UF 8178) also have very dark bellies. As postulated by Hairston, since the dark-bellied forms occur in adjacent areas, at least to the south (rabunensis), southeast (melaventris), and west (teyahalee), the dark-bellied populations on the periphery of the range of shermani may represent intergradation between shermani and these dark-bellied races of P. jordani.

Bishop (1941: 18-19) recorded a series of ten specimens from

near Aquone, west of the Nantahala Mountain range, that he regarded as intergrades between Plethodon shermani and Plethodon glutinosus. At that time, none of the dark-bellied races (except clemsonae) had been described. I have examined Bishop's specimens (CNHM 93241-2; 93250-7) and all but one (CNHM 93241) have a great reduction in the amount of red pigment on the legs, as in teyahalee. Their bellies vary from quite dark to fairly light and seem to bridge the gap between the light-bellied shermani and the dark-bellied teyahalee. It would seem best to regard them as intergrades between teyahalee and shermani, but closer to teyahalee. Bailey (1937: 5) reports a series of five specimens taken about half way between Nantahala and Aquone, in which two resembled glutinosus, (presumably these had dorsal white spots), two had reduced red on the legs, and the other lacked both white and red pigment. These probably also represent intermediates between shermani and teyahalee. Specimens of P. j. teyahalee from the west side of the Nantahala River in this area (near Junaluska Gap, UF 8029; 8091; 8174; 8176) all possess small red spots on the legs, as well as the small dorsal white, characteristic of teyahalee (see below).

Hairston and Pope (1948) believed that specimens from Mooney Gap, in the southern part of the range of shermani, represent intergrades between shermani and rabunensis. Six of a series of thirteen fresh specimens (UF 8179; 8184) from near Mooney Gap possess a marked reduction of red on the legs, but they do not tend toward rabunensis in other characters. Their bellies are light and they appear to be well within the range of eleven Wayah Bald shermani (UF 8101; 8106; 8107) in amount of lateral yellow or white guanophore pigmentation. Much more field work is needed to definitely establish intergradation between these two very

distinct subspecies. Martof and Humphries (1955: 246) report shermani from extreme northwestern Rabun County, Georgia. They state that their specimens possess black bellies. These may be intergrades between rabunensis and shermani.

A series of eleven specimens (UF 8393) of typical shermani from Black Gap on the Macon-Clay County line and the record of Bailey (1937) for the Tusquitee Mountains, establishes the presence of shermani on the west side of the Nantahala River. Three specimens from Glade Gap (UF 8032), about three miles west of Black Gap, have very reduced red pigmentation on the legs, and the single adult has a dark belly. A specimen (UF 8410) from near Tuni Gap, to the northwest of Glade Gap, on the Macon-Clay County line, seems to be typical teyahalee, yet Bailey (1937) reports shermani from Weatherman and Tusquitee Balds, two miles further west. These records suggest slight overlap in the ranges of these two forms and this area should be more carefully studied in the future.

More than half of a series of 22 specimens (UF 8301) from Jarrett Knob, on the east side of the Nantahala River, south of Aquone, have red on the legs either very reduced or absent. The belly color is variable, but would appear to be intermediate between the light- and dark-bellied forms.

P. j. teyahalee was previously known only from the type locality, Teyahalee Bald, in the Snowbird Mountains. A comparison of living topotypes (UF 8166; 8168) from over 4000 feet elevation on Teyahalee Bald with specimens from Tuni Gap and Junaluska Gap, mentioned above, indicates that they are the same form. The original diagnosis

of teyahalee does not distinguish it from rabunensis, and it would have to be synonymized with rabunensis were it not for the fact that most specimens may be distinguished from rabunensis by the possession of tiny (less than 0.3 mm. in diameter) white dorsal spots. These spots are similar to those of Plethodon glutinosus from western North Carolina, but are much smaller. Specimens of teyahalee usually possess small red spots on their legs, a character lacking in most rabunensis and glutinosus.

There are no records of teyahalee from the Snowbird Mountains west of Teyahalee Bald. This mountain range extends to the west and joins the Unicoi range, with altitudes high enough to support a member of this group for most of the distance. Intergrades between unicoi and teyahalee may eventually be found somewhere in this mountain range.

P. j. rabunensis (type locality, Rabun Bald, Georgia) is diagnosed as a dark-bellied form possessing lateral white spots. Specimens from areas to the south and east of Rabun Bald (southern Rabun, Union, and Towns Counties, Georgia) have a much greater development of the lateral white spotting. It is apparent that Rabun Bald specimens are intermediate in this character between southern Rabun, Union, and Towns County specimens and melaventris. Thus the type locality of rabunensis is located in a zone of intergradation. However, since the type specimen possesses lateral white spots, characteristic of the Georgia race, the name rabunensis can still be applied to this subspecies.

Specimens of rabunensis with abundant white or yellow spotting are available from: Persimmon (UF 8408), and 12 miles east of

Clayton (UF 8407), Rabun County; Jack Gap, Union-Towns County line (ChM, uncatalogued); and 4 miles east of Margaret, Union County (UF, uncatalogued). These specimens are very similar in appearance to P. glutinosus, and the relationship between the two may actually be very close. The lack of a good systematic character to distinguish between rabunensis (and teyahalee) and glutinosus makes the identification of living specimens difficult and preserved specimens almost impossible. The lack of dorsal spotting on most rabunensis usually serves to distinguish between the two in life, although occasional specimens of glutinosus from areas outside the southern Appalachians appear identical to it. (In certain localities in the Coastal Plain, P. glutinosus may often lack white pigment completely and cannot be distinguished from melaventris.) Specimens of P. glutinosus from near the range of rabunensis that I have examined in life, from Tullulah Gorge, Rabun County, and Potato Patch Mountain, Murray-Gilmer County line, possess small brassy dorsal spots similar to Florida glutinosus. However, all the P. glutinosus from southwestern North Carolina that I have examined possess white dorsal spots. I have collected this white-spotted form of glutinosus living in the same habitat with members of the jordani group at Soco Gap (Swain-Haywood County line), Cove Creek Gap (Haywood County), Max Patch Mountain (Haywood-Madison County line), Cowee Bald (Macon-Jackson County line), Highlands (Macon County) in North Carolina, and at Jocassee (Oconee County), South Carolina. At the first four mentioned localities it was associated with metcalfi, at Highlands it was associated with melaventris, and at Jocassee with clemsonae. One specimen collected at Rabun Bald along with a series of topotypic rabunensis, also appears to represent this form of glutinosus. It has white

dorsal and gular spots, unlike any other specimens in series of rabunensis, but is otherwise indistinguishable from them.

Very likely the series of 34 specimens reported by Bailey (1937: 3) from Blood Mountain, Union County, Georgia (UMMZ 76334-66), are rabunensis, since only two possessed an appreciable amount of dorsal white pigment, their throats are lighter than most glutinosus, and the lateral white pigment is concentrated into a band. This description almost certainly assigns this series to rabunensis, although both Bailey and Hariston and Pope (1948: 275) identified the specimens as P. glutinosus.

P. j. melaventris, an unspotted dark-bellied form, occurs commonly in the area around Highlands, Macon County, North Carolina. As pointed out by Howell and Hawkins (1954), a small percentage (15%) of topotypical melaventris possess lateral white spotting as in rabunensis. Both the extent and frequency of occurrence of this character in the Highlands population are not high enough to negate the usefulness of this character in diagnosing the two forms. Unspotted black-bellied specimens, probably referable to this race have been reported from several localities to the east of Highlands, but the range of this form, both geographic and altitudinal, as well as its apparent sympatric relationship with glutinosus are much in need of investigation. Two living specimens of melaventris from the vicinity of Highlands had dorsal brassy flecks as in clemsonae in life, indicating a low frequency of occurrence of this character in the Highlands population.

P. j. clemsonae was described by Brimley in 1927 on the basis of its distinct dorsal coloration (which usually disappears in pre-

servatives), but was not again generally regarded as valid until Bishop (1941) obtained additional living specimens from the type locality. This is a low altitude form, occurring in the vicinity of Jocassee, Oconee County, South Carolina. It apparently is very closely related to rabunensis and melaventris, and differs from Rabun Bald specimens only in the possession of small brassy guanophores that are scattered over the entire dorsum. No larger white spots are present on back as in glutinosus. Preserved specimens are usually not distinguishable from the other dark-bellied races with lateral white spots.

An important problem which remains to be studied is the extent of intergradation between the light- and dark-bellied races of P. jordani. Hairston (1950) believed he had intergrades between melaventris and metcalfi from the top of the Balsam Mountains near Beech Gap, but it has been shown above that this population is very close to metcalfi. There is much evidence for intergradation between shermani and teyahalee, and shermani may also intergrade with rabunensis. The greatest difficulty in studying this problem is that after years of preservation, changes take place in the intensity of ventral melanophore pigmentation. Moreover, individual variation is considerable and fair-sized samples should be analyzed. Hence one or two specimens may not be of much use in determining the nature of the population occurring at a particular locality. Except for jordani and shermani, which have melanophore gaps in places where the red pigment is located in life, most faded preserved specimens must be identified almost entirely on the basis of locality. This adds to the difficulties for it means that fresh specimens from new localities are of limited value unless they can be compared with other appropriate living specimens. The

fact that P. glutinosus is often almost indistinguishable from some of the dark-bellied forms (especially rabunensis and teyahalee) further compounds the difficulties in conducting systematic studies in the group. P. glutinosus is easily distinguished from the northern light-bellied races of P. jordani, but appears to be more similar morphologically to the southern dark-bellied races than the two groups of races of P. jordani are to each other. There is evidence of intergradation between the dark- and light-bellied races of P. jordani and they replace each other geographically, indicating a subspecific relationship. P. glutinosus, on the other hand, is known to occur sympatrically with several of the races of jordani without any evidence of interbreeding. According to King (1939: 551), P. glutinosus and P. j. jordani occur together on Gregory Bald, and metcalfi, clemsonae, and rabunensis have been collected in the same locality as glutinosus by the writer (see above). Hairston (1951) also reports slight altitudinal overlap between glutinosus and shermani. On the basis of his field experience with unicoi, Dr. Grobman (personal communication) believes that this form is altitudinally separated from glutinosus on the north slope of the Unicoi Mountains in the vicinity of Stratton Gap. As yet, there are no data on this subject for teyahalee. In general, the northern light-bellied races are altitudinally separated from P. glutinosus (Hairston, 1951) and the localities in which they occur together may happen to be in the narrow zone of overlap between the two species. However, I feel that extreme caution should be exercised in interpreting the type of negative data presented by Hairston. In my experience, a locality that has been intensively collected has often yielded a species of Plethodon that was previously

believed to be absent. P. glutinosus is often much less common than P. jordani where the two occur together, and can easily be overlooked, even though a thorough search is made. It seems to me very unlikely that there is competition between the two for space, food, or some other environmental factor. It seems much more likely that there are other limiting environmental conditions that restrict the altitudinal distribution of the two species.

It is certainly not impossible that P. glutinosus may be found to be subspecifically related to one of the southern dark-bellied subspecies of P. jordani. Two of four specimens identified as glutinosus, from a locality near Highlands, Macon County, North Carolina (UF 8271), possessed in life a slight amount of red pigment on the legs. They were not collected within the range of any race of jordani that possesses red pigment, so they hardly could be considered hybrids or intergrades. Yet the presence of small red spots (similar to those found on teyahalee) on the legs of glutinosus in the southern Appalachians may be considered further evidence for the close relationship between P. glutinosus and the dark-bellied races of P. jordani. Possibly introgressive hybridization has occurred, or perhaps, teyahalee may eventually be shown to intergrade with both shermani and glutinosus. As yet, no one has made a careful transect from the higher altitudes in the Snowbird Mountains in which teyahalee occurs, down into lower glutinosus territory. A transect of the type done by Hairston (1951) on several other races of jordani would be most valuable. At present, since there is no good evidence of intergradation between the two, P. glutinosus and P. jordani are still considered distinct species. It is possible that the close morphological similarity between P. glutinosus

and southern P. jordani is the result of parallel evolution rather than close relationship, as suggested by Hairston and Pope (1948: 276). Grobman (1944) even places the two species in separate groups within the section of the genus containing the Eastern Large Plethodons, but this interpretation is not followed here.

Plethodon kentucki, described by Mittleman (1951: 105) as a member of the jordani group from southwestern Kentucky, has been shown by Clay, Case, and Cunningham (1955) to be based on specimens of P. glutinosus. I have examined the type series and agree with their interpretation. Many of these specimens still possess traces of the large dorsal, lateral, and gular spots characteristic of glutinosus. Most of the type series no longer is tagged so it is impossible to determine which specimens were designated as types by Mittleman. CSNH 1521A was designated as the holotype of P. kentucki, CSNH 1521B the allotype, and 1521C-J as paratypes. There are now only three specimens in a series of 16 (Mittleman designated only 10 as types) that are tagged ("H," "I," and "J") and there is no specimen of the sex and measurements given for the holotype. It is therefore impossible to determine which of these specimens Mittleman designated as the holotype. This may become an important problem in allocating the name in future systematic work on raciation in P. glutinosus, but, for the present, it does not have to be considered further.

Plethodon jordani jordani Blatchley

Plethodon jordani Blatchley (1901: 762). Dunn (1920: 131). Dunn (1926: 145-6). Brimley (1927: 10). Bishop (1928: 159). Pope (1928: 2-3).

Weller (1931: 29). Bailey (1937: 6). King (1939: 551-3). Bishop (1943: 261-4). Grobman (1944: 294). Wood (1947a: 185-8). Hairston and Pope (1948: 266-78). Deevey (1949: 1367-9)

Plethodon jordani jordani Blatchley. Hairston (1950: 271). Hairston (1951: 266-74).

Type:- Dunn (1926: 145) states that the type specimen was originally in the collection of W. S. Blatchley, but that it has been destroyed. It was collected at Mt. Collins or Indian Pass, Sevier County, Tennessee, by L. E. Daniels.

Diagnosis:- A light-bellied subspecies of Plethodon jordani possessing red cheeks in the adult and red dorsal spots in the young. Dorsal and lateral white spots are usually absent, except in juveniles.

Range:- The Great Smoky Mountains of North Carolina and Tennessee (figure 22). The eastern-most records of this race are White Rock Mountain (now Mt. Cammerer) near the town of Mt. Sterling, Haywood County, North Carolina (Dunn, 1926: 146) and on the east slope of Mt. Sterling (UF 8141). There are specimens in the GSMNP collection representing many localities along the crest of the Smoky Mountains (North Carolina-Tennessee state line) from Mt. Cammerer to Gregory Bald, at the west end of the Great Smoky Mountains National Park. This form apparently occurs at higher elevations throughout the Park, except in the southeast corner where it is replaced by metcalfi. Intergrades between the two forms are known from Hyatt Ridge (Hairston, 1950: 263) and Chiltoskie Ridge. The lowest altitude from which this race has been reported is 2500 feet on the slopes of Mt. LeConte, Sevier County, Ten-

nessee (Bishop, 1943: 261).

Description:- This form is characterized by its bright red cheeks. The dorsal and lateral surfaces of the animal are black and the underside is grayish, varying from fairly light in the young to somewhat darker in the adults. The young possess dorsal red spots which are usually arranged in two rows, one on either side of the midline of the anterior half of the back. These are present on most individuals under 30 mm. in snout-vent length, but traces of the red dorsal pigmentation may occasionally occur on specimens up to 50 mm. in snout-vent length. Most young individuals also have red cheeks. The red pigment of the dorsal spots of the young appears to be the same as the red cheek pigment in adults. Both occur in gaps in the melanophore background. There is considerable variation in the amount of red pigment on specimens from the central portion of the Smokies, where large series are available. Some have the red restricted to the upper half of the cheeks, most have the red confined to the sides of the head, but in a few, the red pigment extends ventrally onto the chin, posteriorly on the shoulders, and 10% of the specimens from Indian Gap also have small red spots on the front legs. Most young specimens have small brassy flecks on their eyelids, but these disappear in older individuals. The young often possess small lateral spots on the anterior sides, but these also seem to disappear with age, so that most adults lack guanophore pigmentation, except in the iris of the eye. More than half the adults examined possessed brassy iridic guanophores.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 4 to 12 in each series, increasing in number

with larger size (see figure 16). This form is moderate in size, adults rarely attaining a length over 70 mm. in snout-vent length. Sexual maturity is reached between 45 and 55 mm. in snout-vent length.

Plethodon jordani metcalfi Brimley

Ambystoma jeffersonianum (Green). Rhoads (1895: 402). Brimley (1912: 136).

Plethodon metcalfi Brimley (1912: 138-9). Dunn (1917: 604-6). Fowler and Dunn (1917: 23). Dunn (1920: 131-2). Breder and Breder (1923: 14-5). Bishop (1924: 96). Pope (1924: 2). Brimley (1926: 79-80). Dunn (1926: 148-51). Noble (1927: 4). Bishop (1928: 160). Walker (1934: 190). Bailey (1937: 6-8). Rankin (1937: 176, 180). Green (1939: 49). King (1939: 553-4). Brimley (1940: 6-7). Bishop (1943: 264-6). Green and Richmond (1944: 256). Grobman (1944: 289-92). Snyder (1946: 174). Hairston and Pope (1948: 266-78). Hoffman and Kleinpeter (1948a: 107). Hoffman and Kleinpeter (1948b: 605). Deevey (1949: 1367-9). Hairston (1949: 53-5). Bogert (1952: 16-30).

Plethodon metcalfi metcalfi Brimley. Mittleman (1948: 416-8).

Plethodon jordani metcalfi Brimley. Hairston (1950: 271). Hairston (1951: 266-74).

Type:- USNM 49682, collected near Sunburst, Haywood County, North Carolina, at an altitude of about 3500-4000 feet, in late May, 1912, by Franklin Sherman and C. S. Brimley.

Diagnosis:- A light-bellied subspecies of Plethodon jordani lacking guanophores and lipophores.

Range:- From Cowee Bald, Jackson-Macon County line, Hyatt and Heintooga Ridges, Swain County, and Cataloochee Divide, Haywood County, North Carolina, southeast in the Balsam Mountains to Mt. Pisgah, thence northeast in the Blue Ridge Mountains of western North Carolina and adjacent Tennessee to White Top Mountain and Mt. Rogers in southwestern Virginia (figure 22). Also recorded from Burke's Garden, Tazewell County, Virginia, by Hoffman and Kleinpeter (1948b: 605).

Description:- P. j. metcalfi is the only light-bellied subspecies that lacks both guanophores and lipophores in the adult. This race has the most reduced ventral melanophore pigmentation of any subspecies of P. jordani. The sides and back often have a reduction of black pigment resulting in a lighter over-all appearance than any of the other subspecies. One small juvenile from near Mt. Pisgah (UF 8108) possessed small dorsal guanophore flecks in life. Very large specimens occasionally possess a small amount of white pigment scattered through melanophore gaps on the sides and/or belly, but these guanophores are never concentrated into groups to form white spots as occur regularly in teyahalee, rabunensis, and unicoi. Guanophores are usually absent from the iris.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 4 to 14 in each series, similar to P. j. jordani. This is the smallest race, the largest specimen examined is 66 mm. in snout-vent length, but few adults attain a length over 60 mm. Sexual maturity is reached between 40 and 45 mm. snout-vent length.

Plethodon jordani shermani Stejneger

Plethodon shermani Stejneger (1906: 559-62). Brimley (1912: 138). Dunn (1920: 131). Dunn (1926: 146-8). Bishop (1928: 160-1). Pope (1928: 4-5). Bailey (1937: 4-5). Grobman (1944: 294-6).

Plethodon glutinosus shermani Stejneger. Bishop (1941: 18-9). Bishop (1943: 253-6). Wood (1947b: 188). Wood (1947c: 273-4).

Plethodon shermani shermani Stejneger. Pope and Hairston (1948: 106-7). Hairston and Pope (1948: 274-5). Deevey (1949: 1367-9).

Plethodon jordani shermani Stejneger. Hairston (1950: 271). Hairston (1951: 266-74). Martof and Humphries (1955: 246).

Type:- USNM 36214, collected near Wayah Gap (on the Franklin side of the Gap), Macon County, North Carolina, on August 24, 1904, by Franklin Sherman. See Brimley (1912: 138) for correction of originally designated type locality.

Diagnosis:- A light-bellied subspecies of P. jordani with large red spots on the legs.

Range:- From northwestern Rabun County, Georgia, north in the Nantahala Mountains of Macon County, North Carolina to Tellico Gap; west to Tusquitee and Weatherman Balds, Cherokee County, and Black Gap, Clay County, North Carolina (figure 22).

Description:- The brilliant red legs of typical specimens of this race make it one of the most strikingly beautiful North American salamanders. The dorsum is black and the underside light in the young, becoming grayish in the adult. There are usually a few small lateral yellow or white guanophore spots, most numerous just behind the front limbs. The

young possess dorsal red spots similar to those of P. j. jordani young. The red on the legs of the adults is usually most abundant on the proximal half of the limbs. In specimens with the red on the legs reduced, it is generally reduced on the hind limbs to a greater extent than on the front legs. Populations on the periphery of the range often have dark bellies and reduced red on the legs.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth vary from 3 to 13 in a series and the ontogenetic increase in number is very similar to jordani. A moderate sized form, with dimensions similar to P. j. jordani.

Plethodon jordani unicoi, new subspecies

Type:- UF 8162, an adult female, collected along the trail to Haw Knob from Whiggs Meadow, North Carolina (Graham County)-Tennessee (Monroe County) State line, between 5000 and 5300 feet, on August 17, 1955, by Richard M. Johnson and Richard Highton.

Diagnosis:- A light-bellied subspecies of Plethodon jordani with lateral white guanophore spots.

Range:- Known only from Whiggs Meadow, Haw Knob, Little Haw Knob, Johns Knob, Stratton Gap, and Beech Gap, at elevations over 4000 feet in the Unicoi Mountains along the Tennessee-North Carolina State line (figure 22).

Paratypes:- Graham County, North Carolina-Monroe County, Tennessee State line: UF 8162 (18) same data as holotype; UF 8030 (15), Haw Knob Trail; UF 8303 (26), Whiggs Meadow; UF 8306 (8), Little Haw Knob; UF 8275 (3),

between Mud Flat and Whiggs Meadow; UF 8312 (4), UF 8316 (3), Johns Knob; UF 8283, 0.7 miles south of Stratton Gap; UF 8305 (5), 0.9 miles north of Stratton Gap; UF 8161 (7), 1.3 miles north of Stratton Gap; and UF 8213, 8214 (2), Beech Gap. Tennessee, Monroe County: UF 8310 (2), 1 mile west of Stratton Gap.

Description of the type in life:- Snout to anterior angle of the vent, 54 mm.; snout to posterior angle of the vent, 58 mm.; total length, 114 mm. 16 costal grooves. 7 vomerine teeth on each side. Melanophore gaps on chin and between front legs. Numerous small white spots on sides (now faded after preservation). No guanophores on dorsum, in eye or on eyelids.

Variation (based on 26 specimens examined in life):- Nine (35%) possess small dorsal guanophores (as in teyahalee); one has two small red spots on one front leg; 13 (45%) possess small brassy or white flecks on the eyelids; and all but one possess lateral guanophores. The average belly pigmentation of this series may be compared with the other races of P. jordani by referring to table VII.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth vary from 5 to 12 in a series. A small race, the largest specimen examined is 59 mm. in snout-vent length. Sexual maturity is reached between 40 and 45 mm.

Plethodon jordani melaventris Pope and Hairston

Plethodon metcalfi Brimley (1912: 139). Pope (1928: 4). Chamberlain (1928: 51). Coker (1939: 10-1). Chadwick (1940: 50). Bishop 1943: 264-6).

Plethodon clemsonae Brimley. Grobman (1944: 293-4).

Plethodon shermani melaventris Pope and Hairston (1948: 107). Hairston and Pope (1949: 266-78). Hairston (1949: 53). Deevey (1949: 1367-9). Gordon and Smith (1949: 175).

Plethodon metcalfi clemsonae Brimley. Mittleman (1948: 417).

Plethodon jordani melaventris Pope and Hairston. Hairston (1950: 272). Gordon (1952: 679). Schwartz (1953: 156). Howell and Hawkins (1954: 32-6). Howell (1954: 42-3). Hoffman and Hubricht (1954: 193). Schwartz (1954: 296-8).

Type:- CNHM 47614, an adult male collected at Highlands, Macon County, North Carolina, at an altitude of 3800 feet, on July 27, 1946, by Alexander Pope.

Diagnosis:- A dark-bellied subspecies of Plethodon jordani that typically lacks both guanophores and lipophores.

Range:- Specimens assigned to this form have been reported from Swannanoa, Buncombe County (Grobman, 1944, fig. 5), and Burkemont Mountain, Burke County (Hoffman and Hubricht, 1954) south through Polk, Henderson, Transylvania, southern Jackson, and southeastern Macon Counties, North Carolina, and northern Greenville, Pickens, and Oconee Counties, South Carolina (figure 22).

Description:- The variation in a series of 138 topotypes has been studied by Howell and Hawkins (1954: 32-6). 61 living specimens I have examined from the vicinity of Highlands usually lack iridic guanophores (92%), dorsal guanophores (97%), and lateral guanophores (82%), but all specithat possessed these guanophores had them present in very reduced number. In most cases they could be seen only with the aid of a microscope. The

belly is dark (see table VII), but there is often a reduction of melanophores on the chin, and the chin is almost always much lighter than the belly.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 4 to 17 in a series, tending to increase slightly in number with the size of the animal, as in P. j. jordani. This is a large race; the maximum size recorded is 78 mm. in snout-vent length (Howell and Hawkins, 1954: 33). Sexual maturity is reached between 50 and 55 mm. in snout-vent length.

Plethodon jordani rabunensis Pope and Hairston

Plethodon shermani Stejneger. Howell (1909: 131).

Plethodon glutinosus (Green). Bailey (1937: 3).

Plethodon clemsonae Brimley. Grobman (1944: 293-4).

Plethodon shermani rabunensis Pope and Hairston (1948: 106-7). Hariston and Pope (1948: 274-5). Hairston (1949: 53). Deevey (1949: 1367-9).

Plethodon metcalfi clemsonae Brimley. Mittleman (1948: 417).

Plethodon jordani rabunensis Pope and Hairston. Hairston (1950: 272).

Type:- CNHM 47697, an adult female, collected at Rabun Bald Mountain, Rabun County, Georgia, on August 3, 1946, by members of the C. H. Pope family, at an altitude between 4200-4600 feet.

Range:- Known from Rabun, Union, and Towns Counties in northeastern Georgia (figure 22). Also reported from Habersham County, Georgia, by Mittleman (1948: 418). Specimens from the type locality appear to be intermediate between rabunensis and melaventris.

Diagnosis:- A dark-bellied subspecies of Plethodon jordani with lateral yellow or white spots. These may be so large that adjacent spots unite to form a continuous lateral band.

Description:- Pope and Hairston (1948: 107) state that in their original series, the chief variation was in the amount of lateral white spotting. They state that 15% of their specimens lacked the white lateral and cheek spotting characteristic of this race. However, most of their specimens were collected in 1939 and had been preserved for a number of years. They apparently examined only ten specimens in life. I have examined living specimens from several localities on the north slope of Rabun Bald Mountain and a large proportion of the specimens possess a small amount of lateral and cheek white guanophore spotting. It is, however, poorly developed compared to specimens of this form from the south and west of the type locality. In the latter, the lateral guanophore pigment is very abundant, and often adjacent spots coalesce into a lateral "band" of yellow or white pigment. A small proportion, 2 of 14 (14%) of a series of specimens from Brasstown Bald also have small dorsal guanophore spots, as in teyahalee.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 5 to 13 in a series. This is the largest race, adult specimens approaching the size of glutinosus and yonahlossee. The largest specimen I have examined, from Brasstown Bald, is 82 mm. in snout-vent length. Sexual maturity is probably reached between 55 and 60 mm. in snout-vent length.

Plethodon jordani teyahalee Hairston

Plethodon metcalfi Brimley (1912: 139).

Plethodon glutinosus (Green). Bailey (1937: 3).

Plethodon jordani teyahalee Hairston (1950: 269-72).

Type:- UMMZ 100807, an adult male, collected on Teyahalee Bald, Graham-Cherokee County line, North Carolina, at an altitude of 4525 feet, on August 23, 1949, by Nelson G. Hairston.

Diagnosis:- A dark-bellied subspecies of Plethodon jordani with lateral white or yellow spots, usually with small red spots on the legs, and with very small (0.1-0.3 mm.) white spots on the dorsum.

Range:- Known from Tuni Gap, Clay-Macon County line; near Junaluska Gap, Macon-Cherokee County line; and from Teyahalee Bald in the Snowbird Mountains, along the Cherokee-Graham County line, all in North Carolina (figure 22). Intergrades between teyahalee and shermani occur in the vicinity of Aquone, on the east side of the Nantahala River, in Macon County, North Carolina.

Description:- This race is distinguished on the basis of the presence of small dorsal white spots. These are of a different color than those of clemsonae, and resemble the dorsal spots of glutinosus, except that they are much smaller. The mean size of ten spots measured at random in 11 living specimens range from 0.12 to 0.21 mm., with an average of 0.16 mm. The size of these spots is smaller than in any sample of Plethodon glutinosus I have examined. The red spots on the legs are usually not more than 0.5 mm. in diameter. The lateral spots may be yellow or white, and are not as large as those of rabunensis from the

southern portion of its range, although they are comparable in size to those from Rabun Bald. The same type of spotting that appears on the sides may also be present on the chin.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth vary from 4 to 12 in a series. The largest specimen examined, from the type locality, measures 76 mm. in snout-vent length. Sexual maturity is apparently reached between 45 and 55 mm. in snout-vent length.

Plethodon jordani clemsonae Brimley

Plethodon clemsonae Brimley (1927: 73-5). Brimley (1940: 7). Bishop (1941: 20). Bishop (1943: 239-42). Grobman (1944: 293-4).

Plethodon shermani clemsonae Brimley. Hairston and Pope (1948: 274). Hairston (1949: 53). Deevey (1949: 1367-9).

Plethodon jordani clemsonae Brimley. Hairston (1950: 272). Hairston (1951: 266-74).

Type:- USNM 83849, a male, collected at Jocassee, Oconee County, South Carolina, at an altitude of 1200-1500 feet, by J. A. Berly, on April 8, 1927.

Diagnosis:- A dark-bellied subspecies of Plethodon jordani possessing numerous small dorsal brassy guanophores.

Range: Known only from the vicinity of the type locality, Jocassee, Oconee County, South Carolina (figure 22).

Description:- I have examined only six specimens of this subspecies in life. There is apparently considerable variation in the frequency of

the brassy dorsal spotting. In some specimens it virtually covers the dorsum, while in others it is somewhat reduced. This pigmentation contrasts markedly with that on the lower sides, which consists of small guanophore spots. In the specimens I have examined, these were white in color. Presumably this form is similar to melaventris in size, number of vomerine teeth, and costal grooves. Dr. Albert Schwartz of the Charleston Museum has completed a study of variation in this form and his information should be available in the near future.

Plethodon glutinosus

This species is the most widely distributed of the Eastern Large Plethodons. Workers have long realized that P. glutinosus is quite variable throughout its range. For example, Bishop (1943: 19) states that he believed each of several salamanders, including Plethodon glutinosus, to be " a complex of species or subspecies requiring additional study before its components can be properly delimited." During the last twelve years, three populations of Plethodon glutinosus have been described as separate subspecies. The first, P. g. albagula, was described by Grobman (1944) based on a series of light-chinned examples from the region of the Balcones Escarpment of Texas. In 1949, Allen and Neill described the populations occurring in southeastern Georgia and peninsula Florida as another subspecies, P. g. grobmani. In 1951, Mittleman described P. g. chlorobryonis, based on material from the Coastal Plain of North Carolina. The range of each race, as delimited by the above authors, is quite small, and the remainder of the species, including animals from every physiographic province in which this

species is known, is currently assigned to the typical subspecies, P. g. glutinosus.

The difficulties in studying geographic variation in P. glutinosus are mainly due to the fact that much of the apparent variation in this species, as well as its close relatives, involves pigmentation characters. Most of these pigments are altered by preservatives so that a study of living specimens is necessary in order to obtain accurate information on geographic variation. The recent studies of Hairston and Pope on P. jordani have shown the value of the examination of living specimens from the entire range of a species. The same method was attempted by the writer with P. glutinosus, but much greater difficulties are involved in dealing with a species that occurs over most of the eastern United States, from New York and Illinois south to Florida and Texas. Herpetologists from every state in the range of the slimy salamander were contacted and informed of the study and a request was made for living specimens from each region so that animals from the entire range of the species could be compared. A great many interested persons responded to the request and sent me living specimens. As a result, during the last four years, I have examined slimy salamanders from all but two of the states in which it is known to occur. However, there remain many regions from which I have not had a sufficient number of specimens to obtain a clear picture of the variation within its glutinosus population. Several collecting trips have been made by the writer in order to fill in some of these gaps, but there are so many areas, including whole physiographic provinces, from which data on series of living specimens are not yet available, that the knowledge of the systematics of this

species is still fragmentary. It is felt, however, that some progress has been made and the results, admittedly tentative and incomplete, are presented below.

In comparing living specimens from various parts of the range of this species, it is apparent that there is much individual variation within populations, but very few consistent differences are present between animals from different regions. I have been unable to find any additional characters that vary geographically, other than those previously discussed by Grobman (1944), Neill (1948), Allen and Neill (1949), or Mittleman (1951). All of these characters have been evaluated using both living and preserved specimens.

P. g. albagula is distinguished on the basis of the reduction of the melanophore pigmentation on the chin. As noted by Brown (1950), the characteristic light chin of albagula may occur in a few populations of glutinosus in other parts of the range. Specimens with light chins seem to be especially abundant in the Blue Ridge Province of Virginia. The data that Grobman (1944: 283) presents, indicate, however, that the great majority of P. glutinosus, other than those from Texas, may be distinguished from albagula on the basis of chin pigmentation. A study of additional material from Texas, not seen by Grobman, raise additional problems in connection with the Texas populations that make it difficult to determine the proper systematic position of albagula. These data will be discussed below.

P. g. grobmani was diagnosed on the basis of the color and size of its dorsal and lateral spots, lower costal groove count, and small size. The subspecies, P. g. chlorobryonis was characterized by a re-

duction of dorsal white spots, the color of the lateral spots, by small "orange-gold dots" on the venter, reduced number of vomerine teeth, and smaller average size than other populations of P. glutinosus.

Thurow (1951) has shown that the "orange-gold dots" mentioned by Mittleman are actually hedonic glands found in male glutinosus from its entire range, and the writer has observed the color to change in individuals that were kept alive for some time, presumably due to the accumulation of the secretion of the gland. These glands sometimes occur in females as well as males, and in both sexes the color ranges from clear or colorless to bright orange. There is seasonal variation in the color of these glands, as well as individual variation within a population collected at a single time, but I have seen no evidence of geographic variation in this character.

The range of P. g. chlorobryonis was indicated by Mittleman (1951) to include most of the North Carolina Coastal Plain below the 100-foot contour line. He also believed that the range of this subspecies almost certainly extends into South Carolina. Specimens that he considered intermediate with P. g. glutinosus are from the lower Coastal Plain of adjacent Virginia, from Granville and Wake Counties in the Piedmont of North Carolina, and from Charleston and Berkeley Counties in the lower Coastal Plain of South Carolina.

Schmidt (1953: 34) has recently restricted the type localities of two synonyms of P. glutinosus, Salamandra variolata Gilliams (1818), and Salamandra cylindracea Harlan (1825), to Charleston, South Carolina. Salamandra variolata was originally described as inhabiting the "southern states," but Gilliams (1818: 461) states that the specimens on

which the description of S. variolata were based were received from the "Florida Party." Since they were apparently collected by a person residing in Florida, or an expedition to Florida, this state would appear more likely to be the type locality of S. variolata than South Carolina.

Harlan (1825) states that the specimens on which he based the description of Salamandra cylindracea were sent to him by Dr. Blanding of Camden, South Carolina, who collected other herpetological specimens referred to in the same paper in the vicinity of Camden, South Carolina. Camden would therefore be a better choice for a restricted type locality than Charleston, South Carolina.

Allen and Neill (1949) give the range of P. g. grobmani as "from northern Emanuel and Screven counties, in the Georgia Coastal Plain, southward to Pinellas and Hillsborough counties, Florida, eastward to the Savannah River in Georgia, and westward approximately to the eastern border of the Dougherty Plain in Georgia." This would include Savannah, Chatham County, Georgia, within the range of P. g. grobmani. Indeed, specimens from adjacent Effingham County, Georgia, are designated as paratypes of this form. If this is the actual range of grobmani, then this name is preoccupied by Salamandra albopunctata Vallenciennes (in Dumeril and Bibron, 1854), type locality, Savannah, Georgia. Vallenciennes also described Salamandra elongata in the same paper in which he described S. albopunctata, but failed to designate a type locality. This form was also probably based on specimens from the southeastern Coastal Plain, but it will probably never be necessary to designate a type locality for it, as there are several earlier names available for southeastern Coastal Plain P. glutinosus.

There are, then, six names available for the Plethodon glutinosus of the southeastern Coastal Plain:

Salamandra variolata Gilliams, 1818 (type locality, probably Florida).

Salamandra cylindracea Harlan, 1825 (type locality, probably Camden, South Carolina).

Salamandra albopunctata Valenciennes, 1854 (type locality, Savannah, Georgia).

Salamandra elongata Valenciennes, 1854 (type locality not designated).

Plethodon glutinosus grobmani Allen and Neill, 1949 (type locality, Half-mile Creek Swamp, about one-half mile northeast of Silver Springs, Marion County, Florida.)

Plethodon glutinosus chlorobryonis Mittleman, 1951 (type locality, 13 miles north of New Bern, along U. S. Highway 17, Craven County, North Carolina).

The subspecific identity of several Coastal Plain populations of P. glutinosus must be determined in order that the name Salamandra variolata, which has priority over all the other more recent names, can be correctly assigned. In order to attempt to correctly apply the above names and to determine the number of valid subspecies of glutinosus in the Atlantic Coastal Plain, living specimens have been obtained from the type localities, as well as from many other places in the region. The characters studied will be analyzed separately below.

Number of costal grooves:- Both Allen and Neill (1949: 112) and Mittleman (1951: 11) state that in southeastern Coastal Plain, P. glutinosus possesses one or two costal grooves less than more northern populations,

which usually have 16 costal grooves. Data on the number of costal grooves and trunk vertebrae in several geographic samples of P. glutinosus are given in table VIII. To avoid counting the same characteristic (number of body segments) twice, costal groove counts are not included in the table for any of the specimens for which vertebral counts are listed.

The modal number of trunk vertebrae in each sample is 17 and the corresponding number of costal grooves is 16. The only variation appears to be in the percentage of individuals with one segment more or less than the mode. In the Texas sample, 11 (8%) possess 18 vertebrae, and there are none with 16 vertebrae. On the other hand, in the southeastern Coastal Plain, there is a slight tendency to possess one less segment than the modal number. Radiographs indicate that 9 of 22 (41%) specimens from peninsula Florida have 16 trunk vertebrae, but this is apparently an unusual sample, for only 20 of 150 (13%) additional specimens have 15 costal grooves. These slight differences may indicate the beginning of differentiation in the populations concerned, but the differences are not of the magnitude claimed by previous workers.

Size:- Both Allen and Neill (1949: 112) and Hittleman (1951: 111) noted the reduction in size in southeastern Coastal Plain glutinosus. Size is a difficult character to analyze in cold-blooded vertebrates, unless large series of specimens are available, so that an accurate estimation of maximum size or size at maturity can be obtained. Another difficulty results from the fact that the average size of mature animals varies from season to season, for as the group of immature animals begins to mature, the average size of sexually mature adults will be lowered. As growth continues, the average size of mature animals will increase

TABLE VIII

GEOGRAPHIC VARIATION IN BODY SEGMENTATION OF PLETHODON GLUTINOSUS

Locality	Number of costal grooves			Number of trunk vertebrae		
	15	16	17	16	17	18
Coastal Plain:						
Virginia				4	25	1
North Carolina				3	7	1
South Carolina		11		2	15	2
Georgia	3	36	1			
Florida (peninsula)	20	126	4	9	12	1
Alabama	1	4				
Mississippi	3	13				
Other physiographic provinces:						
New York					4	
New Jersey		16			2	
Pennsylvania					3	
Maryland		1			1	
Virginia		14		1	8	
North Carolina	1	31				
South Carolina				1	19	
Georgia		14	2			
Ohio		5				
Kentucky	1	6				
Tennessee	1	31	5			
Arkansas	1	27	1			
Texas					120	11

throughout the remainder of the year. That this factor is important in Florida P. glutinosus was shown by the writer (in press). As yet we have very little knowledge of the life history of P. glutinosus in other parts of the range and have no basis on which to make comparisons of the average size at maturity. In Florida, in the fall, most specimens over 45 mm. in length are mature, whereas in the summer, most under 55 mm. are immature. I have examined mature specimens of P. glutinosus from the southern Appalachian Mountains that were between 45 and 50 mm. in snout-vent length. At present, there is no evidence to support the contention that there is a difference in size at maturity between Florida and Appalachian mountain P. glutinosus. This does not rule out the possibility that differences in size at maturity between different populations do exist, but more information on the life history of this species outside Florida is needed to confirm this premise.

The maximum size of over 700 peninsula Florida specimens that I have measured is 69 mm. in snout-vent length (before preservation). The largest Virginia Coastal Plain specimen I have measured is 72 mm. in snout-vent length (after several years of preservation). In small samples from many other localities in the range of this species (Texas, Indiana, New York, New Jersey, Pennsylvania, Maryland, and the Piedmont and Blue Ridge Provinces of Virginia, North Carolina, South Carolina, and Georgia), specimens between 70 and 80 mm. in snout-vent length are common, and the largest specimen examined (UF 8112, collected 5.2 miles south of Sunburst, Haywood County, North Carolina), a male, was 86 mm. in snout-vent length before preservation. Clearly, the maximum size of peninsula Florida glutinosus is less than most other populations, but maximum size obviously cannot be used as a systematic character with

which to assign or identify individual specimens.

Vomerine teeth:- Mittleman (1951: 109) published the vomerine tooth counts on the type series of P. g. chlorobryonis. He pointed out that they were much lower than most counts on P. g. glutinosus. He also suggested that the vomerine count in grobmani might be expected to be even lower than those in chlorobryonis. Vomerine tooth counts were made on 32 specimens from the Coastal Plain of Virginia, 13 specimens from the Coastal Plain of North Carolina, and 269 specimens from peninsula Florida. The data obtained are shown in figures 14 and 15. In addition, the series of 125 specimens that Pope and Pope (1948) used in their study of this character in montane Virginia glutinosus were also examined by the writer. My counts on this series were essentially the same as the Popes' counts. It is obvious that adult Coastal Plain Virginia and North Carolina specimens have fewer vomerine teeth than either peninsula Florida or Virginia mountain specimens. An examination of the figures shows another difference between the three populations. In each sample there is an ontogenetic increase in the number of vomerine teeth. A t-test on the difference between the rate of increase (slope) of the equations for the Virginia mountain and Florida samples, shows that the probability of obtaining a difference as great or greater than that observed by chance alone is less than .0001. In spite of this significant difference in the rate of increase in the number of teeth with growth, there is wide overlap in the number of teeth in similar size groups of the two populations. In the Coastal Plain Virginia and North Carolina samples, there is a further reduction, both in number of teeth and the rate of increase with growth. Some slight overlap between the Virginia mountain and Coastal Plain Virginia and North Carolina sam-

ples remain, although a majority of adult specimens of each form could be segregated by a striaght line separating the dots representing the two populations. For example, a line passing through the point (snout-vent length = 45, vomerine teeth = 16) and the point (snout-vent length = 70, vomerine teeth = 18) would separate 69 of 75 (92%) Virginia mountain specimens 45 mm. and over in length from 33 of 35 (94%) Coastal Plain Virginia and North Carolina specimens 45 mm. and over in length. The condition in samples from the Virginia Piedmont is unknown, but the intermediate Florida sample shows wide overlap with both of the above samples. A significant biological difference between the P. glutinosus of the three areas is obvious, yet this character could hardly be used as a key character to separate either of the Coastal Plain samples, or the Florida and the Virginia mountain samples into separate subspecies. The observed differences in the number of teeth may be the result of a gradual clinal change that is not usually recognized by the systematist as a basis for erecting subspecies.

Size of dorsal spots:- The size of the dorsal spots of living or freshly preserved specimens was measured with the aid of an ocular micrometer (1 micrometer unit = 0.0685 mm.). Since the size of the dorsal spots increase with growth, the ratio of the average size of ten dorsal spots chosen at random to the snout-vent length was used as a basis of comparison. Specimens of different lengths in the same sample usually show similar ratios when compared in this manner. The data obtained are shown in table IX.

It is apparent that in the Atlantic Coastal Plain there is a decided decrease in the size of the dorsal spots from north to south. There is wide overlap between every adjacent population and nowhere is

TABLE IX. GEOGRAPHIC VARIATION IN DORSAL SPOT SIZE OF P. GLUTINOSUS

Locality	Ratio Mean Spot Size / Snout-vent length x 100							Actual mean (not grouped)
	1.0-4.9	5.0-8.9	9.0-12.9	13.0-16.9	17.0-20.9	21.0-24.9	over 25.0	
Coastal Plain:								
Virginia	2	12	1	1				7.2
North Carolina	1	7	5					8.3
South Carolina		3	12	2	1			11.1
Georgia	1	2	12	4	8	3	3	15.7
Florida (Peninsula)		1	7	10	16	10	2	17.9
Florida (Panhandle)			1	4	3	11		20.5
Alabama				2	1	2		19.5
Mississippi			1		1			14.6
Louisiana				1				14.3
Other Provinces:								
New York	1	1		1		1		12.9
New Jersey						1	1	24.5
Pennsylvania				1	1			17.7
Maryland					1	2		22.6
Virginia		1	2	4	3	2	1	16.8
North Carolina								
Piedmont			4	7	1			13.5
Blue Ridge	1	12	18	5			1	10.4
South Carolina		1	7	14	5	1	1	15.1
Georgia		1	1	3	2	1	1	16.5
Tennessee			7	7	6	3	2	16.8
West Virginia					1	1		22.2
Indiana			1	4		2		17.4
Texas		8	2					8.6

there apparent an abrupt change from small to large spots. This character, at least in the Atlantic Coastal Plain, would appear to represent an internal cline. There is not sufficient material available from the Gulf Coastal Plain, except for west Florida, to determine whether or not there is another decrease in the size of dorsal spots to the west. In other parts of the range of glutinosus, from which material is available, the average size of the dorsal spots appears to be fairly large, except for Texas and North Carolina specimens. In North Carolina, the average size of the dorsal spots for 12 specimens from the Piedmont is 13.5, while the average size of 37 specimens from the Blue Ridge Province is 10.4. The available specimens would not support the contention that there is a west to east reduction in size of spots toward the Coastal Plain, since the Piedmont series has spots averaging slightly larger than those in the mountains.

One of the diagnostic characters given for chlorobryonis is the small size of its dorsal spots. Unquestionably, the size of the dorsal spots of specimens from the Coastal Plain of Virginia and North Carolina is much reduced. This reduction is approached by specimens from Texas, the Blue Ridge Province of North Carolina, and the Coastal Plain of South Carolina. Because of the clinal nature of the variation of this characteristic in the Coastal Plain, it cannot be used as a systematic character to separate the North Carolina and Virginia populations of Coastal Plain glutinosus from the remainder of the species, although it may be considered evidence that these populations show further biological differences from many other populations of glutinosus.

All but one of the specimens in the Coastal Plain Virginia

sample are well-preserved specimens in the Carnegie Museum Collection. The one living specimen has a mean spot size to snout-vent length ratio of 6.4, lower than most North Carolina Coastal Plain specimens. In the preserved Carnegie Museum series, only the dorsal spots of specimens in which they are well-defined and clearly visible are included, so that they are almost certainly comparable to the living material on which the remainder of the table is based.

One of the characters that Allen and Neill (1949: 112) used to diagnose P. g. grobmani was "back with tiny scattered dots of a metallic golden color." Data on the geographic variation of the color of dorsal spots will be given below, but it is obvious that the size of these spots in populations from the Coastal Plain of Georgia and Florida are well within the range of many other populations of P. glutinosus.

Color of dorsal spots:- The color of the dorsal spots is one of the diagnostic characters used in the original description of P. g. grobmani by Allen and Neill (1949: 112). The dorsal spots of specimens from southeastern Georgia and northern peninsula Florida were described as a "metallic golden color." This character was described as being the most conspicuous diagnostic feature of P. g. grobmani. It is true that a very large proportion of specimens from the range of grobmani possess dorsal spots containing a large proportion of brassy guanophores. This type of dorsal spotting is not restricted to specimens from this area, however. Sinclair (1950: 200) pointed out that specimens from Shelby County, in western Tennessee, possess dorsal spots that are similar in color to those described for grobmani. I have examined living speci-

mens with as heavy brassy flecking as occurs in topotyic grobmani, from many localities outside its range as defined by Allen and Neill. Specimens in this category were collected in the Piedmont of Georgia (Fulton County); the Blue Ridge Province of Georgia (Murray and Gilmer Counties); the Blue Ridge Province of Tennessee (Monroe County); Greene County, New York; Pike, Monroe and Alleghany Counties, Pennsylvania; as well as many localities in the Coastal Plain of Virginia, North Carolina, South Carolina, western Florida, southwestern Georgia, Alabama, and Mississippi. In some of these localities, only an occasional specimen shows a heavy amount of brassy flecking (e.g. the New York, South Carolina and the Georgia Piedmont samples), but in most of the other localities mentioned, it is the usual condition. This is especially true of specimens from southeastern Tennessee and Potato Patch Mountain, Murray-Gilmer County line, Georgia, where many individuals exceed the usual peninsula Florida glutinosus in amount of brassy flecking.

In spite of the fact that the presence of brassy flecking is not limited to certain southeastern populations, there is considerable evidence that it does not occur throughout the entire range of this species. I have examined more than a dozen living specimens from single localities in the Blue Ridge Province of Virginia, North Carolina, and northeastern Tennessee, as well as the Piedmont Province of North Carolina and South Carolina. In most of these specimens the brassy flecking was extremely reduced or absent and in only about 10% was there a moderate amount of brassy flecking present. In other localities from which I have studied more than a dozen specimens, the usual condition appears to be intermediate, with a moderate amount of dorsal brassy

flecking. P. glutinosus of this type have been examined from central New Jersey (including the vicinity of Princeton, the type locality of P. glutinosus); Cataraugus County, New York; Randolph County, West Virginia; Giles County, Virginia; the Piedmont of Georgia; and eastern Oklahoma.

An objective method of comparing the color of dorsal spots of specimens from different localities was necessary before geographic variation in this character could be successfully analyzed. Two methods were used, both of which have certain advantages and limitations. The first was to compare the actual color of the dorsal spots with a standard color guide. Villalobos and Villalobos (1947) has a decided advantage for analyses of this type because the spots may be compared directly with the color through a small hole punched in the center of each color. In this manner the color (to the naked eye) of the spots of specimens from different localities could be compared with a standard. The same person made all the comparisons under uniform light conditions and the possibility of unconscious bias was reduced by the fact that the person making the comparisons was not informed of the geographic provenance in which the specimens were collected. A disadvantage of this method is due to the fact that specimens with different sized spots, or individuals in which the white guanophore pigmentation was less concentrated, would often appear different in color, although the actual amount of brassy guanophore flecking was similar. To get around this difficulty, a parallel study of the pigmentation was made with the aid of a dissecting microscope.

Specimens that were obtained from various parts of the range were maintained alive in a refrigerator at a temperature of about 11° C. At this temperature, adult Plethodon can survive for a year or two with a moderate amount of care and feeding. The maintenance of a collection of living specimens of this species was necessary in order to compare living specimens from different localities that could not be obtained alive simultaneously. Some loss of material before it could be thoroughly studied occurred, and as a result, a number of specimens that were casually studied on their arrival could not be included in some of the data in the tables because accurate notes on their color or pigmentation were not taken.

The data on the color of dorsal spots indicate a large amount of variation in this character in specimens from a single locality. Three characteristics are measured using Villalobos and Villalobos' color guide. These are hue, lightness value, and degree of chromaticity. Essentially these measure the color, lightness or darkness, and intensity of the color. All three readings were taken from the spots of a given specimen. One way to analyze individual or geographic variation is to compare each measured quality separately.

The color of dorsal spots in P. glutinosus varies from SSO to E (see Villalobos and Villalobos, 1947, for the meaning of the symbols used here), and in addition there are some individuals in which color is lacking (see table X). In specimens in which the dorsal spots appear brassy to the naked eye, the color characteristically ranges from O to YYO. There appears to be little difference in color in samples with reduced brassy and those in which the brassy

TABLE X

THE COLOR COMPONENT OF THE DORSAL SPOTS OF SAMPLES OF PLETHODON GLUTINOSUS BASED ON COMPARISONS WITH VILLALOBOS AND VILLALOBOS (1947)

Sample	SSO	SO	OOS	O	OOY	OY	YYO	Y	YYL	YL	LLY	L	G	GE	E	Gray
Coastal Plain:																
North Carolina				3	5	1	1									
South Carolina				1	2		1									2
Georgia			1	17	7	7	2									2
Florida (Peninsula)			1	56	15	2	1	1								
Florida (Panhandle				14	23	33	19		1							
Alabama				11	2	3										
Mississippi				1	3	1	1									
Louisiana				4	4											
Oklahoma						1										
Other Provinces:																
New York					2		2	1				1				1
New Jersey					4	1										
Pennsylvania				2	6											

TABLE X (CONTINUED)

Sample	SSO	SO	OOS	O	OOY	OY	YYO	Y	YYL	YL	LLY	L	G	GE	E	Gray
Other Provinces:																
Maryland						2	1									
Virginia					5	6	4	6		3	2			1	1	10
West Virginia				1		1	3		4							
North Carolina					6	1				1	1	1	1			6
South Carolina		1	1	2	1	4										19
Georgia	3			4	4	4	3	4								2
Tennessee				8	8	2	3	1	1							
Kentucky-Virginia line				1												
Indiana								1								
Missouri				2												
Arkansas-Oklahoma line							1		1							
Oklahoma						2										
Texas			1		6	4		1								

pigment is abundant. In samples in which the brassy pigment is absent or very reduced (Virginia, North Carolina, and South Carolina Piedmont and Blue Ridge specimens) there is a tendency for the color to be slightly more green (usual range O to LLY) as well as a high percentage of specimens which do not show any color to the naked eye. There is wide overlap in the color of spots of specimens in which the brassy pigment is present and those in which it is absent, but the essential difference in the absence of color in those individuals that have white spots is often detected by this method.

The lightness value ranges from 10 to 20 (see table XI), with very little difference between samples from different regions. The sample means vary from 14.5 to 19.0 with no apparent geographic trends. A significant difference may exist between samples with or without brassy flecking, but such a wide overlap exists between the two samples that this character is of little value in distinguishing between the two types.

There is considerable variation in the degree of chromaticity, or intensity of the color, in the various samples (see table XII). The entire range is from Gray to 9°. In this character, there is a decided geographic variation, the brassy flecked populations showing a much greater amount of color than those that usually lack the brassy-type guanophores. It would be difficult to identify specimens on this basis, although there is a significant difference between the two (cf. the Piedmont and Blue Ridge Virginia, North Carolina, and South Carolina samples with the Georgia, Florida, and Alabama Coastal Plain samples). The Tennessee sample is made up entirely of specimens of the brassy

TABLE XI

THE DARKNESS INTENSITY OF THE DORSAL SPOTS OF SAMPLES OF PLETHODON GLUTINOSUS BASED ON COMPARISONS WITH VILLALOBOS AND VILLALOBOS (1947)

Sample	10	11	12	13	14	15	16	17	18	19	20	Mean
Coastal Plain:												
North Carolina				1		2	1	3	2	6		17.3
South Carolina	1			2			1	1	1			14.5
Georgia			2	4	3	2	5	4	9	5		16.3
Florida (Peninsula)			5		11	9	13	16	15	11		16.4
Florida (Panhandle)			2		2	5	4	10	29	39		17.8
Alabama					1	2	4	4	2	3		16.8
Mississippi					1	1		3		1		16.5
Louisiana							1	3		3		17.7
Oklahoma								1				17.0
Other Provinces:												
New York						2	2		2	1		16.7
New Jersey					1		2		1	1		16.6
Pennsylvania						2	4		1			16.0

TABLE XI (CONTINUED)

Sample	10	11	12	13	14	15	16	17	18	19	20	Mean
Other Provinces:												
Maryland								2		1		17.7
Virginia						3	12	11	2	11		17.2
West Virginia							2	1	2	4		17.9
North Carolina					1	3	4	3				15.8
South Carolina		1		2	6	7	2	6	1	3		15.5
Georgia		1				2	4	3	5	9	1	17.5
Tennessee						1	3	5	8	7		17.7
Kentucky-Virginia line										1		19.0
Indiana									1			18.0
Missouri							1		1			17.0
Arkansas-Oklahoma line									2			18.0
Oklahoma							1		1	1		17.7
Texas									4	9		18.7

TABLE XII

THE DEGREE OF CHROMATICITY OF THE DORSAL SPOTS OF SAMPLES OF PLETHODON GLUTINOSUS BASED ON COMPARISONS WITH VILLALOBOS AND VILLALOBOS (1947)

Sample	Grey	1°	2°	3°	4°	5°	6°	7°	8°	9°	Mean
Coastal Plain:											
North Carolina		1		3		1	5				4.5
South Carolina	2		1								0.7
Georgia	2	1	8	5	7	6	6				3.6
Florida (Peninsula)		1	4	15	19	16	18	3	1	3	4.7
Florida (Panhandle)		3	9	24	12	8	33		1	1	4.4
Alabama					5	3	7		1		5.3
Mississippi				1	1	3	1				4.7
Louisiana			1	2	2	1	2				4.1
Oklahoma			1								2.0
Other Provinces:											
New York	1	3	1	1			1				2.0
New Jersey			4				1				2.8
Pennsylvania		3	3		1		1				2.4

TABLE XII (CONTINUED)

Sample	Gray	1°	2°	3°	4°	5°	6°	7°	8°	9°	Mean
Other Provinces:											
Maryland				1							3.0
Virginia	10	3	7	6	3	1	7	1			2.7
West Virginia			1	3	1	2	2				4.1
North Carolina	6	7	3	3			1				1.4
South Carolina	19	8	1	1	1	2				1	1.1
Georgia	2	4	2	4	2		8		1		3.7
Tennessee				1	3		18	1	1		5.8
Kentucky-Virginia line										1	9.0
Indiana			1								2.0
Missouri		1	1								1.5
Arkansas-Oklahoma line			2								2.0
Oklahoma				1	1		1				4.3
Texas				5	1		5				4.5

flecked type, and the Georgia Piedmont and Blue Ridge sample includes both types.

The results of the examination of the actual spots under the magnification of a dissecting microscope show a variation that corresponds to the data obtained from comparisons made with the color charts. The weakness of these data lies in the fact that the assignment of specimens to each category was somewhat subjective. The specimens I used for standards are now preserved and so it will be impossible for other workers to repeat the work without obtaining living specimens from the localities from which individuals were used as a basis of comparison. I chose a typical specimen from Torreya State Park, Liberty County, Florida, as an example of an animal with a large amount of brassy flecks in each dorsal white spot. A specimen from 5 miles east of Davidson, Cabarrus County, North Carolina, was chosen as the other extreme, completely lacking brassy flecks in the dorsal spots. Specimens that showed a very slight amount of brassy pigment, usually at the borders of the dorsal white spots were regarded as "slightly brassy." Others, that had a moderate amount of brassy flecking in the white spots were placed in an intermediate category. In a few specimens, usually those with very small spots, no white guanophores could be seen, only the brassy type were present. These were included under the heading, "brassy only." These data are summarized in table XIII (most of the specimens from Tennessee included in this table belong to the white-spotted northeastern Tennessee sample rather than the southeastern Tennessee brassy-spotted population).

The results of these data on the color of the dorsal spots

TABLE XIII

GEOGRAPHIC VARIATION OF DORSAL PIGMENTATION IN PLETHODON GLUTINOSUS

Sample	White only	Slightly brassy	Moderately brassy	Heavy brassy	Brassy only
Coastal Plain:					
Virginia					1
North Carolina	3	3			11
South Carolina	5	5	4	3	
Georgia	5	16	10	11	5
Florida (Peninsula)			4	25	5
Florida (Panhandle)			1	14	1
Alabama				6	
Mississippi		2		4	
Louisiana				2	
Other Provinces:					
New York	1		2		1
New Jersey			3		
Pennsylvania				6	
Maryland			3		
West Virginia		1	1		
Virginia	11	5			
North Carolina	24	21	5		
South Carolina	11	12	4		
Georgia	1	7	3	4	
Tennessee	1	16	4	4	1
Missouri	2				
Oklahoma		1	1	1	
Texas		10			

are difficult to interpret because of the paucity of material from a great many areas. The only large series are from the southeastern states. The condition in the northeastern portion of the range of glutinosus appears to be more similar to that of Florida specimens than it is to the color of Piedmont and Blue Ridge specimens from Virginia, North Carolina and South Carolina. The data are sufficient to refute Allen and Neill's suggestion that the brassy condition is limited to Georgia and Florida Coastal Plain specimens, for most individuals from New York, New Jersey, Pennsylvania, northern Georgia, and southeastern Tennessee have a moderate to large amount of this type of flecking. Whether the Piedmont and Blue Ridge specimens from Virginia, North Carolina, and South Carolina are different enough from animals in the remainder of the range to warrant nomenclatorial recognition on the basis of this character remains to be determined. This may be the case, but a study of much more material from the northern and mid-western states is needed before a decision can be reached with any degree of certainty.

Abundance of lateral pigment:- Grobman (1944: 282) has pointed out that there is a north-south cline in the amount of white lateral pigment in this species. Specimens from the southeastern Coastal Plain have large lateral spots and in many adults the spots coalesce to form a lateral band of white pigment. Specimens from the southern Appalachians show a reduction in the size of the lateral spots, and farther north, the lateral spots are no larger than those on the dorsum. Grobman also pointed out that some Texas specimens possess a large amount of lateral pigment that forms a band on the sides of adults.

One other difference has been noted in the lateral pigmentation of glutinosus in the northern portion of its range, compared to southern specimens. In a large proportion of animals from New York, New Jersey, Pennsylvania, Maryland, and West Virginia, the pigment in the center of lateral spots seems much more concentrated than that on the edges of the spots, whereas in the south, where the spots are usually larger, the pigment is more evenly distributed. This character is probably also clinal in nature, but has not been analyzed in detail.

It is difficult to measure and evaluate the size of the lateral spots, since two adjacent spots lose their identity as they fuse during growth. I have not made measurements of the size of lateral spots, but superficial examination of specimens from different regions confirms the observations of earlier workers. The lateral band seems to be most prevalent in specimens from the Virginia, North Carolina, and South Carolina Coastal Plain, as well as some Texas populations. Allen and Neill (1949: 113) report that specimens from Burke, Jefferson, Washington, Glascock, and Richmond Counties, Georgia, also have an abundance of white pigment on the sides. I have not examined living specimens from any of these counties.

Color of lateral pigment:- The color of the lateral spots was used as a diagnostic character in the original descriptions of both grobmani and chlorobryonis. The lateral spots of grobmani were described as being grayish, while those of chlorobryonis are described as being greenish-white or yellow-green. A study of the color of the lateral spots similar to that made on the dorsal spots is summarized in tables XIV, XV, and XVI. The data on comparisons of lateral spots with

TABLE XIV

THE COLOR COMPONENT OF THE LATERAL SPOTS OF SAMPLES OF PLETHODON GLUTINOSUS BASED ON COMPARISONS WITH VILLALOBOS AND VILLALOBOS (1947).

Sample	S-OOS	O	OOY	OY	YYO	Y	YYL	YL	LLY	L	LLG	LG	GGL	G	GE	E	T	TC	Gray
Coastal Plain:																			
Virginia			1																
North Carolina		7	10	12	6														2
South Carolina			3	2	5	2													6
Georgia		6	7	5	11	2				1					1	1			20
Florida (peninsula)		8	4	7	5	1	3	1				1	1	1	1				50
Florida (panhandle)		8	3	2	5		2			1		2	1	2	7	5	1		53
Alabama		2	1	2	3	1				2	2								4
Mississippi		2	2		2														2
Louisiana			10																1
Oklahoma				1															
Other Provinces:																			
New York	1	1			2	1	1												3
New Jersey		1	1	2			1												

TABLE XIV (CONTINUED)

Sample	S-OOS	O	COY	OY	YYO	Y	YYL	YL	LLY	L	LLG	LG	GGL	G	GE	E	T	TC	Grey
Other Provinces (continued):																			
Pennsylvania	2	1		4															1
Maryland				1	1														1
Virginia	1				4	3	4	2	1	2	2				2			1	12
West Virginia						2	1		1			1		1					3
North Carolina				8	1			1	1	1				1					6
South Carolina	8	7	2	5		2	1												7
Georgia	3	2	1	1	2		4	2	5	1									8
Tennessee					2	3	8	3	1	1	1			1					2
Indiana				1															
Missouri		2																	
Arkansas-Oklahoma line				1	1														
Oklahoma			1	1	1														2
Texas			9	12	4														

TABLE XV

THE DARKNESS INTENSITY OF THE LATERAL SPOTS OF SAMPLES OF PLETHODON GLUTINOSUS BASED ON COMPARISONS WITH VILLALOBOS AND VILLALOBOS (1947).

Sample	9	10	11	12	13	14	15	16	17	18	19	Mean
Coastal Plain:												
Virginia						1						14.0
North Carolina			2	3	11	10	12	7	3	1		14.3
South Carolina	1	2	1	4	5	1		3				12.6
Georgia		1	2	9	16	10	6	2	6	1		13.8
Florida (Peninsula)	1		2	4	9	20	19	14	10	2	2	14.8
Florida (Panhandle)					6	18	25	18	18	5	3	15.5
Alabama				2	1	3	3	4	2		2	15.3
Mississippi						3	1	1	3			15.5
Louisiana				1	1	3	3	2	1			14.6
Oklahoma						1						14.0
Other Provinces:												
New York					1	1	2	1	1	3		16.0
New Jersey							1			1	3	18.0

TABLE XV (CONTINUED)

Sample	9	10	11	12	13	14	15	16	17	18	19	Mean
Other Provinces (Continued):												
Pennsylvania				3				2	3			14.9
Maryland			1		1				1			13.7
Virginia					3	6	4	7	3	5	5	16.1
West Virginia									3	2	4	18.1
North Carolina				1		4	1		2			14.6
South Carolina			2	3	4	9	6	4	2		1	14.3
Georgia			1		1	2	3	9	5	2	2	16.0
Tennessee					2	1	6	5	5	2	1	15.9
Indiana											1	19.0
Missouri							1	1				15.5
Arkansas-Oklahoma line								1		1		17.0
Oklahoma							1	2	1	1		16.4
Texas		1	2	6	9	2	2	2	2			13.3

TABLE XVI

THE DEGREE OF CHROMATICITY OF THE LATERAL SPOTS OF SAMPLES OF PLETHODON GLUTINOSUS BASED ON COMPARISONS WITH VILLALOBOS AND VILLALOBOS (1947)

Sample	Gray	1°	2°	3°	4°	5°	6°	7°	8°	9°	Mean
Coastal Plain:											
Virginia		1									1.0
North Carolina	2	24	9	2							1.3
South Carolina	6	8	4								0.9
Georgia	20	30	4								0.7
Florida (Peninsula)	50	25	6	2							0.5
Florida (Panhandle)	53	28	8	5							0.6
Alabama	4	10	3								0.9
Mississippi	2	4	1			1					1.4
Louisiana	1	8	1	1							1.2
Oklahoma			1								2.0
Other Provinces:											
New York	3	1	2	1	1		1				2.0
New Jersey				1	2		1			1	5.2

TABLE XVI (CONTINUED)

Sample	Gray	1°	2°	3°	4°	5°	6°	7°	8°	9°	Mean
Other Provinces (continued)											
Pennsylvania	1	3	2	1	1						1.8
Maryland	1	1	1								1.0
Virginia	13	7	9	5							1.2
West Virginia	3	1	1	4							1.7
North Carolina	6	10	3		1						1.0
South Carolina	7	17	7	1							1.1
Georgia	8	10	4	3							1.6
Tennessee	2	12	5	2	1						1.5
Indiana						1					5.0
Missouri		1	1								1.5
Arkansas-Oklahoma line			1		1						3.0
Oklahoma	2		1			1	1				2.6
Texas		5	9	6	4	2					2.6

Villalobos and Villalobos' Color Atlas indicate that a large proportion of Florida specimens lack color and appear gray, while a majority of North Carolina Coastal Plain specimens, as well as those from Texas, are found in the yellow to orange range. In most other samples there is a large amount of variation in the color of the lateral spots. There is slight variation in the lightness of the spots, but wide overlap between most samples. The amount of chromaticity appears to be quite variable, with the Florida and Virginia samples having an especially large proportion of gray individuals. Although there may be significant biological differences between these samples in the various aspects of the lateral guanophore pigmentation, there certainly would seem to be no justification in naming either the North Carolina Coastal Plain or the Florida and Georgia Coastal Plain populations as recognizable subspecies on the basis of this character.

Studies of the lateral pigment with the aid of a dissecting microscope indicate that the yellow pigmentation is not to the presence of brassy guanophores, but rather due to an actual difference in the color of the non-iridescent guanophores that appear to be the same type as those found on the dorsum, where they are always white. In classifying the color of the lateral spots, three categories were used, white, intermediate (yellowish-white), and yellow. The data on this character are tabulated in table XVII. In the Atlantic Coastal Plain there appears to be an internal cline in the amount of yellow pigment, with a reduction in intensity from North Carolina to Florida. The Texas sample has lateral pigment that is extremely yellow, but the average condition of specimens in the remainder of the range is intermediate between the two extremes. A large amount of individual varia-

TABLE XVII

GEOGRAPHIC VARIATION IN THE COLOR OF LATERAL SPOTS OF PLETHODON GLUTINOSUS

Sample	White	Yellowish-white	Yellow
Coastal Plain:			
Virginia			1
North Carolina		1	16
South Carolina	3	3	12
Georgia	16	9	13
Florida (Peninsula)	26	5	1
Florida (Panhandle)	12	3	1
Alabama		3	3
Mississippi	2	3	1
Louisiana		1	1
Other Provinces:			
New York		2	2
New Jersey	1	2	
Pennsylvania	2	3	1
Maryland		2	1
West Virginia		2	
Virginia	6	6	2
North Carolina	22	8	13
South Carolina	12	10	4
Georgia	9	3	3
Tennessee	20	3	1
Missouri		2	
Oklahoma	1		2
Texas	1		9

tion is present in this character within adults of each population. There is also an ontogenetic change in the appearance of lateral guanophore pigment, judging from the appearance of young specimens in populations in which the normal adult spotting appears yellow. Young individuals of all samples I have examined possess white lateral guanophores and the change to yellow occurs at an earlier age in populations in which the normal adult condition is yellow.

Absence of guanophores:- Specimens that completely lack dorsal and lateral guanophore pigmentation are occasionally found in samples of glutinosus from various parts of its range. In at least two areas, this characteristic is present in a large proportion of specimens and thus deserves special mention. Neill (1948) reports that in Jasper County, South Carolina, there exists a population of P. glutinosus in which 100% of the specimens are characterized by the complete absence of guanophore spotting. In adjacent areas, individuals in which guanophore pigmentation was absent were also recorded, but they occur with the normally spotted individuals. I have examined two series of P. glutinosus from Jasper County and in both series, numbering 16 and 7 respectively, every specimen was entirely black. Two of 12 specimens that I have examined from a locality in Dorchester County, South Carolina, also lacked guanophores, confirming the observations of earlier workers (Cope, 1889: 142; Schmidt, 1924: 67; Neill, 1948) that the unspotted type also occurs in the Charleston area. Several deviations described by Neill (1948) for South Carolina Coastal Plain material are not confirmed by this study. In specimens examined by me, no consistant differences in the number of costal grooves, proportional length of tail, parasphenoid teeth, melanophore pigmentation, size, head

shape, or structure of the vent in males could be detected. In collecting specimens at the locality mentioned by Neill (1948), 7 miles north of Tillman, Jasper County, South Carolina, I was impressed by the unusual agility of the animals in escaping the collector, as well as the apparent delicacy of the skin, compared with other Coastal Plain glutinosus. Whether these differences are real or not, they would be difficult to measure objectively, although histological examination of the integument of the dark form might reveal structural differences other than the absence of white spots.

Another Coastal Plain locality in which a large proportion of specimens lack guanophore spotting was discovered in Florida. On the east side of the St. Johns River in Volusia County, about 1 mile south of Astor, there is a population of P. glutinosus in which about half (14 of 30) of the specimens are entirely black. On the west side of the St. Johns River, in three nearby localities in Lake County (within 10 miles of Astor) only one of 107 specimens showed a complete absence of dorsal and lateral white spotting, so common on the east side of the river. Apparently the gene or genes responsible for this condition occur with small frequency in some glutinosus populations, but have become fixed in the Jasper County, South Carolina population and are present in much greater than usual frequency in the Volusia County, Florida population.

Grobman (1944: 281) states that "there is, apparently, a large glutinosus devoid of white marking which ranges from the Cumberland Plateau. Localities for this form are in Bibb, Chilton, Lawrence, and St. Clair Counties, Alabama; Chatooga, Dade, DeKalb, Fulton, Gilmer, and Murray Counties, Georgia; Edmonson, Harlan, Laurel, Morgan, and Whitley

Counties, Kentucky; Pontotoc and Webster Counties, Mississippi; Avery, Buncombe, Cherokee, Graham, Haywood, Macon, Polk, Swain, and Transylvania Counties, North Carolina; and Claiborne, Cumberland, Davidson, DeKalb, Fayette, Fentress, Rhea, and Sevier Counties, Tennessee." I have examined living specimens from Fulton County and the Murray-Gilmer County line, Georgia; Harlan County, Kentucky; Haywood, Macon, and Swain Counties, North Carolina; and Davidson and Rhea Counties, Tennessee. Every specimen that I have examined from these counties, as well as many others from other counties in the region of the supposed unspotted form, possess both dorsal and lateral guanophore spots. Apparently the difference noted in preserved specimens is not present in life, and may merely result from the disappearance of the spots as a result of preservation.

Abundance of melanophore pigmentation on chin:- In 1944, Grobman described a Texas population of Plethodon glutinosus as a separate subspecies, P. g. albagula. It was diagnosed as a "race of glutinosus in which the arrangement of the black pigment to form small compact circles has been broken down in the gular region, thereby presenting a gross appearance of a lighter throat than that found in the typical race of glutinosus." An examination of Grobman's map of the distribution of glutinosus shows a gap of approximately 120 miles between the McLennan County and the Upsur County records of glutinosus in Texas. If this hiatus actually represents an area in which glutinosus no longer occurs, then the population found along the Balcones Escarpment in south-central Texas would seem to be isolated from its nearest relatives and differentiation might be expected. However, specimens from two localities in

the region of the Balcones Escarpment were tentatively referred by Grobman to typical P. g. glutinosus. These are from Bell and Blanco Counties, and the latter record, based on only one specimen (CM 6129), is only about 20 miles from localities at which paratypic albagula were collected.

Brown (1950: 32) assigned specimens from Bell, Bexar, Blanco, Comal, Hays, Kendall, Real, and Travis Counties to P. g. albagula, although Grobman had indicated that specimens from two of these counties had dark chins. Brown also remarked that "the status of Plethodon glutinosus albagula as a valid subspecies needs further investigation. White throated forms have been reported from other areas supposedly in the range of P. g. glutinosus."

Several series of recently collected specimens from Texas, have confirmed the fact that both light- and dark-chinned forms occur in the region described as being inhabited by albagula. A series of 24 specimens (JSM 667-676, UF 8085 (4), 8342 (4), 8343 (6)) from a sink hole about 5 miles southwest of Austin, Travis County, are typical of Grobman's description of albagula. They possess very light chins and in life, had an abundance of yellow lateral pigment, which, except in very young specimens, formed a continuous lateral band of guanophore pigment. This condition was mentioned by Grobman (1944: 284) as an additional characteristic of albagula, although he pointed out that this type of pigmentation was not entirely limited to albagula. The color of this lateral band in life is unlike that of glutinosus from other parts of its range. Grobman also mentioned that the dorsum of albagula is almost devoid of white pigment spots. The living specimens

did not lack dorsal white spots, but the spots were very small in relation to the size of the animal compared to most glutinosus. In addition to these characters, these specimens of albagula were found to differ from glutinosus in that a rather high proportion possess 18 trunk vertebrae. The vertebrae of one small specimen could not be counted accurately, but of the remaining 23, seven have 18 trunk vertebrae, four have 17/18 (the 18th trunk vertebra bears the sacral rib on one side, the 19th on the other side), and 12 possess 17 trunk vertebrae. Two freshly preserved specimens (UF 8009) from the Guadalupe River bluff, 2 miles south of Sattler, Comal County, are identical in appearance with the above series. Both possess 17 trunk vertebrae.

Available freshly preserved specimens from two other localities, UF 7143 (3), 7145 (1), from the head springs of Mill Creek, 5 miles northeast of Vanderpool, Bandera County, and UF 3413 (6) from Bull Creek, west of Austin, Travis County, are strikingly different from albagula. The sides of these specimens, although preserved for a shorter period than many of the albagula, possess only a few small scattered white spots. In none of these specimens was there any tendency toward a coalescence of the lateral spots into a band. The chins of most of these specimens are as dark as their bellies. In only three young individuals are they slightly lighter than the bellies, but in none are the chins as light as in albagula of comparable size.

Dr. Grobman has kindly examined the specimens mentioned and has informed me that the series on which he based the description of albagula were similar to the specimens that were collected at the sink hole, about 5 miles southwest of Austin. The dark-chinned samples obviously do not fit the description of albagula and are thus similar

to the specimens he examined from Bell and Blanco Counties.

Additional material from Texas, not examined by Grobman (1944), was borrowed from Bryce C. Brown, Ottys Sanders, and the Strecker Museum. Most of the Strecker Museum's collection is so faded and stained due to many years of poor preservation, that it is impossible to allocate some specimens to either form. A series of 15 specimens (SM 16, 247-57, 1002, 1055) from Helotes, Bexar County, cannot be determined, although at least 11 have 17 trunk vertebrae. Two others probably have 17, while the other two are too small to make accurate counts from the radiographs.

One specimen (SM 5087) from Austin, Travis County, appears to have reduced melanophore pigmentation on the chin (although its chin now appears dark due to staining).

SM 5213-16 and 5223, from Frio Canyon, Real County, may definitely be assigned to the dark-chinned form. They are presumably the specimens on which Strecker (1935: 32) based his Real County record, that Grobman (1944: fig. 3) included as a possible albagula locality on the distribution map. They are not albagula, but the dark-chinned form. Three have 17 trunk vertebrae, the other two probably also have 17 trunk vertebrae.

A large series of 40 specimens from San Marcos, Hays County (SM 1837, 3241-2, 3244-76, 4963-7) are in poor condition. 27 have 17 trunk vertebrae, 8 probably also possess 17 trunk vertebrae, and the vertebrae in the remaining specimens could not be counted. The melanophores on the chins of some of the specimens could not be discerned, but in most they appear to be much reduced as in albagula. One specimen

(SM 3244), however, possesses as dense a melanophore network on the chin as on the belly. In most of the larger specimens of this series, it appears that white pigment was abundant on the sides, as in albagula. Four other specimens from San Marcos (OS 613, BCB 115, 2087, and 2423) also have light chins and 17 trunk vertebrae. Although all of the San Marcos specimens for which accurate counts are available possess 17 trunk vertebrae, on the basis of their light chins they appear to be referable to albagula. Grobman (1944: 283) designated 31 specimens from San Marcos as paratypes of albagula.

Three specimens (BCB 116-8) from Deep Eddy, west of Austin, Travis County, have dark chins and two (117-8) have 17 trunk vertebrae. BCB 5269-73 were taken from a cave near McNeil, Travis County. All five have dark chins and two have 18 trunk vertebrae, the other three 17.

Ten specimens (SM 3162-3, BCB 7015-22) from Fern Bank, near Wimberly, Hays County, have light chins of the albagula type. Two have 18 vertebrae, the other eight 17. The presence of 18 vertebrae in only two other series from Texas, one of which is not albagula, would seem to indicate that the high proportion of 18 trunk vertebrae in the one sample collected 5 miles southwest of Austin, is either of local occurrence or the result of random sampling error and not of taxonomic significance. Three specimens (CNHM 37666-8) from Wimberly were designated as paratypes of albagula.

A series of 16 specimens from the vicinity of another paratypic locality of albagula (BCB 3431-40, woods near Spring Creek, 11 miles northeast of Boerne, and BCB 4983-8, from Schneider Cave, 14

miles northeast of Boerne, Kendall County) are unusual in having a large amount of ventral guanophore spotting. All but three have light chins of the albagula type, and all (except 4987, that is too small to obtain an accurate vertebral count) possess 17 trunk vertebrae.

BCB 2234, near Cibolo Creek, 18 miles northeast of San Antonio, Bexar County, in the vicinity of the type locality of albagula, has 17 trunk vertebrae and a light chin. It also has a large number of lateral spots, but it is a young individual and the spots have not yet coalesced to form a band.

Several other specimens from the vicinity of Austin, Travis County (BCB 301, 1161-2, Zilker Park, Austin; BCB 799, Lake Austin; BCB 1163-70, 1956-7, Austin Caverns, west of Austin; BCB 1277-78, Barton Creek, south of Austin; and UF 3414 (10), 3460 (1), junction of Barton and Little Barton Creeks), include specimens with both light and dark chins. All except BCB 1163, 1166-8, and 1277-8 which could not be accurately counted, possess 17 trunk vertebrae.

It is difficult to analyze the distribution of the two forms, if indeed, there actually are two forms represented, because of the incomplete data on the characteristics of many of the specimens examined. Based on the freshly preserved University of Florida material, it would seem that we are dealing with two different forms, as different from each other as most species of Eastern Large Plethodons. The lateral band of albagula is very similar to the type found in the yonahlossee group. The light chin, a characteristic of the yonahlossee group, is also found in albagula. On the other hand, some Texas populations seem to have both light- and dark-chinned specimens represented. I

have not examined living specimens of the Texas dark-chinned form, although the preserved specimens appear to be very similar to P. g. glutinosus. Living albagula are very distinct from P. g. glutinosus, and it may be that albagula is a valid form, possibly a distinct species more closely related to the yonahlossee group than to the glutinosus group, or else intermediate between the two groups. This would not rule out entirely a subspecific relationship with glutinosus, if intergradation could be demonstrated.

Another possible interpretation is that there may be some environmental influence that is acting on certain Texas populations of glutinosus (i.e. albagula), causing them to differ phenotypically from other populations of this species. If this were the case, then most systematists would recognize albagula as an ecotype, not to be given nominal recognition. Grobman (1944: 284) points out that most of the available habitat labels accompanying specimens of albagula mention caves. More recent collections seem to indicate, however, that both types may be found either in or out of caves. Constant temperature conditions in caves might play an important part in producing a different type of pigmentation than that found in animals that undergo their embryonic development outside of caves. Plethodon glutinosus is known to lay its eggs both in and out of caves. Grobman (1944: 282) discusses the possible importance of temperature during embryonic development in the production of lateral pigmentation. Temperature might also have an effect on the number of somites (and vertebrae) in this species.

The Balcones Escarpment separates two major physiographic provinces, the Coastal Plain and the Edward's Plateau section of the

Great Plains. The change in the underlying rocks, vegetation, and rainfall at the Balcones Escarpment is very abrupt (Smith and Buechner, 1947). No correlation is indicated on the basis of the present distributional data, however, since both light- and dark-chinned specimens have been collected on both sides of the Balcones Escarpment (figure 23).

A third possible explanation of the situation, the one reflected by the current nomenclature, is that the two forms are subspecifically related. The puzzling samples from Travis County, in which both light- and dark-chinned specimens, as well as intermediate types appear in one population, could be considered evidence for intergradation between typical P. g. glutinosus and P. g. albagula. According to this interpretation, the specimens from Bell, Blanco, Bandera, and Real Counties might be assigned to P. g. glutinosus, occurring, as they do, to the north and west of the albagula records. Most of the specimens from Hays, Comal, Kendall, and Bexar Counties show the characteristics of albagula, while both typical albagula, typical glutinosus, and intermediates occur in Travis County. Geographic replacement between the two forms is a definite possibility. If the true relationship is found to be subspecific, it may be postulated that the isolation in which albagula differentiated was of considerable duration and that typical glutinosus has only recently reinvaded the region, with only a slight amount of secondary intergradation.

A field study of the species in the area involved is much needed. A comparison of living specimens from the entire region, a study of the life history, ecological requirements, and more information on the distribution of the animals will be needed before the proper

systematic status of the Texas Large Plethodons can be determined. With our present knowledge, it would seem best to propose no change in the existing nomenclature with regard to albagula, pending a study that would clarify its true status.

Wright and Wright (1938: 34) report P. glutinosus from Medina County, Texas, but no specimens seem to be available now from this county. Strecker (1902: 100; 1908: 80) reports the species from Mc Lennan County on the basis of two specimens, one a sight record. Its actual occurrence in this county certainly needs confirmation. If P. glutinosus does not occur in McLennan County, then the gap in the range of Texas glutinosus is greater than indicated above.

Strecker (1915: 55) states that he collected two specimens near Cleveland, Liberty County, in the southeastern Coastal Plain of Texas. Since no other records of P. glutinosus are known for over 150 miles from this locality in any direction, this record should be deleted from the authenticated range of P. glutinosus until it can be verified.

Summary of geographic variation in Plethodon glutinosus:- In most of the characters studied, geographic variation was found to be present. These characters were not chosen at random, however. They were selected for detailed analysis because previous workers had found evidence of geographic variation in them and this had been supported by preliminary observations made by the writer. In a critical study of other characters of living specimens from various parts of the range, I could find no others that could be successfully correlated with geography.

In the number of trunk segments, the differences between

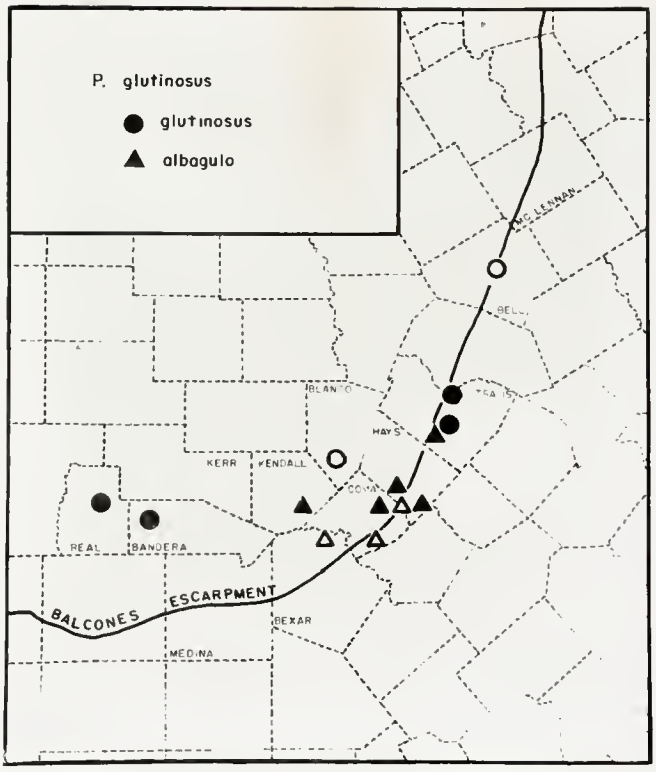

Figure 23. The distribution of the dark-chinned (glutinosus) and light-chinned (albagula) populations of P. glutinosus in central Texas. Solid symbols represent localities from which specimens have been examined by the writer. Hollow symbols represent literature records of Grobman (1944).

geographic samples are very slight, but in the other characters studied, consistent differences between some samples are demonstrable. Southeastern Coastal Plain specimens are significantly smaller than most other P. glutinosus. The number of vomerine teeth is reduced in Florida glutinosus, compared with the Virginia mountain sample, and the North Carolina and Virginia Coastal Plain specimens exhibit a further reduction. The size of the dorsal spots shows clinal variation in the Atlantic Coastal Plain, increasing from north to south. The spot size of other populations, except those in the Blue Ridge Province of North Carolina, and in Texas, appears to be about the same as southern Coastal Plain animals. The color of the dorsal spots is extremely variable, but uniformly white in the southern Piedmont and Blue Ridge Provinces north of Georgia, and uniformly brassy in the Gulf Coastal Plain from Mississippi to Florida. Lateral spots are larger and more yellow in color in the Atlantic Coastal Plain and in Texas. Texas animals usually possess a great reduction in the number of melanophores on the chin.

On the basis of the above data, several tentative conclusions on raciation in P. glutinosus may be suggested. The Texas populations are apparently isolated from the remainder of the species. Living Texas specimens that have been examined differ in several ways from glutinosus in other parts of its range and are the most distinctive of all of the samples of this species studied by the writer. For the present, it would seem advisable to continue to recognize albagula as a separate form, although there remain many questions that must be answered before its correct systematic position can be determined.

Another population that differs from most other P. glutinosus in a number of ways is the one that occurs in the South Carolina, North Carolina, and Virginia Coastal Plain. Its reduced vomerine teeth, small dorsal spots, lateral yellow band of guanophore spots, and small size serve to distinguish a large proportion of these animals from the remainder of the species. No single one of these characters is limited to this population, however, and all but the last appear to be the result of a gradual clinal-type change from south to north in the Coastal Plain, with wide overlap between adjacent populations. Most systematists would not recognize the end products of such a cline as separate subspecies. For those that care to recognize the northern end of this cline as a nominal form, the name cylindracea is available for the South Carolina population. P. g. chlorobryonis Mittleman, based on specimens from the North Carolina Coastal Plain would not appear to be valid, since there is wide morphological overlap between the North Carolina and South Carolina populations.

Similarly, for those who would recognize the southern end of this cline as a separate subspecies, the name grobmani would not be applicable, since it is preoccupied by at least two earlier names, variolata being the oldest. This name would be available for all Coastal Plain P. glutinosus if, in the future, it is shown that these populations should be given racial recognition. At present, there are no known characters, other than size, that would support this thesis. Although, as yet, there is not sufficient reason to recognize a southeastern Coastal Plain race (or races), the information on geographic variation of several characters is extremely suggestive in explaining

some of the distributional problems and relationships of these populations of Plethodon glutinosus.

The Florida and Georgia samples are closer to the non-Coastal Plain samples than are the Virginia and Carolina Coastal Plain populations in every character except maximum size. If the wide-ranging P. glutinosus was first able to adapt itself to the Coastal Plain environment in Georgia (or, perhaps to the west of Georgia), it probably migrated to the northeast into the coastal areas of the Carolinas and southeastern Virginia. There are no records of glutinosus from the Coastal Plain of northern Virginia, the Del-Mar-Va Peninsula, southern New Jersey (south of Ocean County), or Long Island, although Plethodon cinereus has been able to adapt to Coastal Plain conditions in all these areas. It would therefore appear that northeastern Piedmont glutinosus have been unable to move into the Coastal Plain. The fact that Virginia Coastal Plain glutinosus are so different from upland Virginia glutinosus lends support to the theory of a more southerly origin of the former, rather than a close relationship to glutinosus populations in the adjacent Piedmont.

One other interesting situation has been discovered as a result of field work being done in southeastern Tennessee by Mr. Richard M. Johnson. Nicholls (1950: 312) has suggested that there is more than one type of Plethodon glutinosus in eastern Tennessee, but does not describe them. Field work in western North Carolina has indicated that glutinosus of that region are unusual in invariably possessing white dorsal spots. Mr. Johnson has also collected this white-spotted glutinosus at several localities in eastern Tennessee.

In other localities, however, eastern Tennessee glutinosus populations exist in which the amount of brassy flecking is greater than in most Florida specimens. (This type of brassy flecked glutinosus also occurs in northern Georgia at Potato Patch Mountain, Murray-Gilmer County line). It is quite possible that more than one form is represented in this area and it is hoped that Mr. Johnson's field studies will clarify the altitudinal, ecological, and geographic distribution of the two forms, as well as to shed some light on their relationships.

Plethodon glutinosus glutinosus (Green)

Salamandra glutinosa Green (1818: 357). (Type locality probably Princeton, New Jersey)

Salamandra variolata Gilliams (1818: 460). (Type locality, Southern States, probably Florida)

Salamandra cylindracea Harlan (1825: 156). (Type locality, South Carolina, probably the vicinity of Camden)

Plethodon glutinosus (Green). Tschudi (1838: 58). Bishop (1941: 219-32).

Plethodon glutinosum (Green). Gray (1850: 39).

Salamandra albopunctata Valenciennes in Dumeril and Bibron (1854: 81). (Type locality, Savannah, Georgia)

Plethodon variolosum (Gilliams). Dumeril and Bibron (1854: 83).

Salamandra elongata Valenciennes in Dumeril and Bibron (1854: 84) (Type locality not designated)

Salamandra melanoleuca Wied (1865: 130). (Type locality, Nazareth, Pennsylvania)

Plethodon glutinosus glutinosus (Green). Dunn (1920: 131). Bishop (1943: 250-3). Grobman (1944: 278-83).

Plethodon glutinosus grobmani Allen and Neill (1949: 112). (Type locality, near Silver Springs, Marion County, Florida)

Plethodon kentucki Mittleman (1951: 105-8). (Type locality, Big Black Mountain, Harlan County, Kentucky)

Plethodon glutinosus chlorobryonis Mittleman (1951: 108). (Type locality, 13 miles north of New Bern, Craven County, North Carolina)

Plethodon jordani kentucki Mittleman. Schmidt (1953: 37).

Type:- Dunn (1926: 138) states that the type is not known to exist, but that the type locality is obviously Princeton, New Jersey.

Diagnosis:- A dark-bellied, dark-chinned Eastern Large Plethodon with dorsal and lateral guanophore spots, and without red pigment.

Range:- Central New York west to central and southern Illinois, south throughout all the states east of the Mississippi River, except for southern Florida, and the Atlantic Coastal Plain north of southern Virginia. West of the Mississippi River, it occurs in east-central and southern Missouri, the northwestern half of Arkansas, eastern Oklahoma, and extreme northeastern Texas (figure 24). Dark-chinned specimens which may be referable to this subspecies are also known from Real, Bandera, Blanco, Travis, and Bell Counties in the region of the Balcones Escarpment of Texas (figure 23).

Description:- This form is extremely variable and the reader is referred to the above discussion of geographic variation in this species for descriptions. The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 4 to 17 in a series.

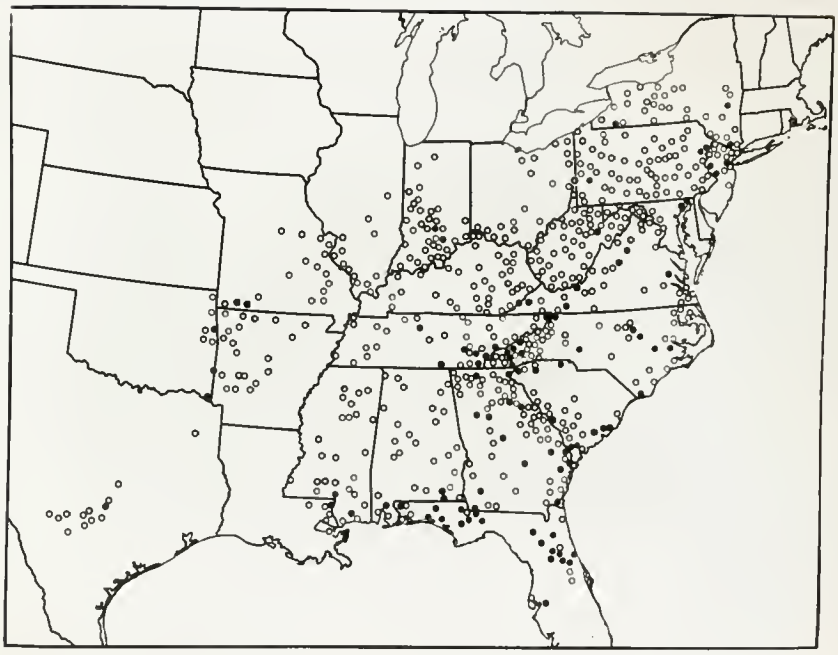

Figure 24. The distribution of Plethodon glutinosus in eastern United States. Solid symbols represent localities from which living specimens have been examined. Hollow symbols represent literature records and localities from which preserved specimens have been examined. See figure 23 for a map of the distribution of the subspecies of P. glutinosus in Texas.

There is geographic variation in size, the largest peninsula Florida specimen (from Eureka, Marion County), is 69 mm. in snout-vent length, while the largest specimen on record (Orton, 1946) is 88 mm. in snout-vent length. Sexual maturity is reached between 40 and 56 mm. in snout-vent length in Florida, but there is little or no information for other areas.

Plethodon glutinosus albagula Grobman

Plethodon glutinosus albagula Grobman (1944: 283). Brown (1950: 32-3).

Type:- CM 9652, an adult male, collected 20 miles north of San Antonio, Bexar County, Texas, on February 24, 1935, by Wesley Clanton.

Diagnosis:- A subspecies of Plethodon glutinosus that differs from the typical race in possessing a reduction of melanophore pigmentation on the chin.

Range:- Known from Bexar, Kendall, Comal, Hays, and Travis Counties, Texas.

Description:- Living specimens from a sink hole, about 5 miles southwest of Austin, Travis County, Texas, besides possessing the diagnostic light chin, also have exceptionally yellow lateral spots, which are often so large that adjacent spots fuse to form a lateral band in adults. The dorsal spots are small and white. As noted above, this population is unusual in the number of trunk vertebrae, so it may not be typical in other respects.

The costal grooves usually number 16, the trunk vertebrae 17. Vomerine teeth range from 4 to 11 in a series. This form is large in

size, the largest specimen examined is 75 mm. in snout-vent length.

SUMMARY

A systematic study of the North American salamander genus Plethodon indicates that there are three major groups in the genus. These are called the Western Plethodons, the Eastern Small Plethodons, and the Eastern Large Plethodons. Special emphasis has been placed on a study of pigmentation characters in living specimens and in the variation in trunk vertebrae measured by means of X-ray photographs. A method of correlating the number of costal grooves with the number of trunk vertebrae has been suggested.

The Western Plethodons are divided into four species groups. The Plethodon vandykei Group, with one species, vandykei, includes three subspecies. The Plethodon vehiculum Group includes two monotypic species, dunni and vehiculum. The third species group includes a single species, formerly known as P. elongatus, for which a new name is proposed, P. productus. The fourth species group of Western Plethodons also contains a single species, P. neomexicanus.

The Eastern Small Plethodons are divided into two species groups, the Plethodon welleri Group and the Plethodon cinereus Group. The first includes two species, welleri and richmondi (with three races). The Plethodon cinereus Group consists of two species, dorsalis with two subspecies, and cinereus with three races.

The Eastern Large Plethodons are divided into three species groups. The P. wehrlei Group includes one species, wehrlei, with three

races. The Plethodon yonahlossee Group includes three species, yonahlossee, ouachitae, and caddoensis. The Plethodon glutinosus Group has two species, jordani with eight subspecies (one, unicoi, is new), and glutinosus with two races.

The Eastern Large Plethodons and the Eastern Small Plethodons are more closely related to each other than either is to the Western Plethodons. The Eastern Small Plethodons appear to be closer to the Western Plethodons than are the Eastern Large Plethodons.

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BIOGRAPHICAL ITEMS

Richard Highton was born on December 24, 1927, in Chicago, Illinois. He graduated from the Bronx High School of Science in New York City in June, 1945. He received the Bachelor of Arts degree with a major in biology from the University College of Arts and Sciences, New York University, in October, 1950.

He entered the University of Florida in September, 1951, and received the Master of Science degree in biology in June, 1953.

He served as a graduate assistant in the Department of Biology at the University of Florida from July, 1952, to January, 1954. From February to June, 1954, he held a graduate fellowship. From September, 1954, to the present, he has been a teaching assistant in the Department of Biological Science. During the summer of 1955, he was employed as a Ranger-Naturalist by the Great Smoky Mountains National Park.

He is a member of the American Society of Ichthyologists and Herpetologists, the Herpetologists League, and Sigma Xi.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of the committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June 4, 1956

C. F. Byers
Dean, College of Arts and Sciences

Dean, Graduate School

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